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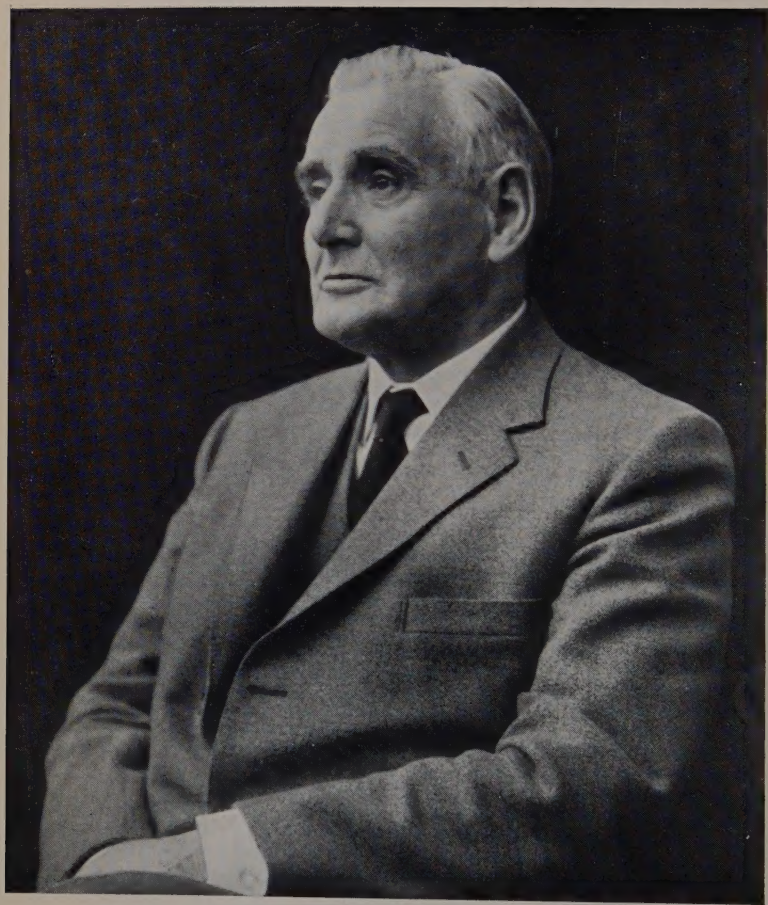
BOTANICAL SOCIETY OF
EDINBURGH //

VOLUME XXXVIII

Papers presented by some of the friends, past
and present colleagues, and former students
of

PROFESSOR J. R. MATTHEWS

on the occasion of his Seventieth Birthday
March 8th 1959



Professor JAMES ROBERT MATTHEWS, C.B.E.,
M.A., F.R.S.E., F.L.S.

FOREWORD.

"Why should anyone's 70th birthday call for notice? There may be an answer; I do not know."

Thus wrote Professor Matthews in a recent letter. Where *his* 70th birthday and the Botanical Society of Edinburgh are concerned the answer is easy. It is simply that the Society desires to honour one who has been intimately associated with it for exactly fifty years in the varying capacities of Student Member, Fellow, Secretary, and President, always striving for the Society's welfare, always happy in the realisation that the Society prospers. Only one as modest as Professor Matthews would fail to understand this and to appreciate that all who have contributed to this volume, financially and otherwise, have expressed their sense of pleasure in being privileged to do so.

But *why* should the Society have had the great good fortune to be served by so loyal a Fellow? That, I do admit, is not so easily understood, nor the question so readily answered. It is partly because Professor Matthews has believed at all times that the Society has had an important part to play in the furtherance of botanical knowledge. No matter whether he was Lecturer in Botany at Birkbeck College, London, or in the University of Edinburgh, or Professor of Botany in the University of Reading or in the University of Aberdeen, always has he firmly maintained that the Society had important contributions to make to the botanical life not only of Edinburgh but also of Scotland and beyond. And part of the answer lies in the fact that being first and foremost a *teacher* he quite instinctively realised that the Society was an excellent vehicle for the spreading of botanical knowledge to the non-professional botanist.

Professor Matthews has made valuable contributions to plant science, notably his works on the origin and distribution of the British Flora. But these are the least of his accomplishments. As an administrator he has few peers; his colleagues in Aberdeen and his botanical friends elsewhere all agree that no Department of Botany in Britain has more increased in stature than has that at Aberdeen during the twenty-five years of his Regius Professorship. The Councils of various Societies—The British Ecological, The Linnean, The Royal Society of Edinburgh—the Councils,

Committees and Governing Bodies (of many of them he has been Chairman) of various Institutions—The Macaulay Institute for Soil Research, The North of Scotland College of Agriculture, The Nature Conservancy, The Scottish Horticultural Research Station, The Scottish Field Studies Association and others—all testify to his wise guidance and to his skill as an administrator. But more important by far than this is the enormous influence he has had as a *teacher*. All who contribute to this volume (they are friends, past and present colleagues, and former students) and every student who has been privileged to train under him will agree that in a quite wonderful way, in lecture room, laboratory, and in the field, he has stimulated their interest in botanical science and has spared himself in no sense to help them along the way. One of his most distinguished former students, my friend George Taylor, the Director of Kew, will speak for many when he says "Professor Matthews more than anyone guided my botanical footsteps and set them firmly in the direction that they have taken. I was under his genial and inspiring tutelage during my four years honours course and I consider that his teaching, in its preparation and presentation, was the best that I have ever experienced".

Personally I am proud to look back over the twenty-five years when I have enjoyed his friendship and powerful encouragement; back in fact to a day in the early Spring of 1934 when he came for the first time into the Department at Aberdeen and found me, utterly confused and humiliated, under a table where some acorns had rolled off a herbarium specimen of a Siamese Oak! Though we may look back, however, we must also look forward, for a 70th birthday, and the consequent retirement from an arduous post filled with great distinction, is not the end of a career. Freedom from much of the burden of administration gives freedom to enjoy the renewal of scientific work, some of the results of which I do not doubt we shall see in future pages of these *Transactions*.

By dedicating this volume of its *Transactions* to Professor Matthews, the Botanical Society of Edinburgh endeavours to express its gratitude, even in small measure, for fifty years of selfless devotion, not only to the Society but to the greater cause of botanical science.

H. R. FLETCHER.

CONTRIBUTION TO THE FLORA OF SUTHERLAND.

BETTYHILL REGION.

By JOHN ANTHONY

(Department of Botany, University of Edinburgh).

Bettyhill is a small village in the north of Scotland, about midway between Cape Wrath and Dunnet Head (Fig. 1). It is situated on a promontory where the Naver—the largest river in the north—enters the sea.

The coast consists of precipitous cliffs with bare bluff headlands and numerous rocky inlets and the two sandy bays of Farr and Torrisdale. The coastal region is the more interesting for inland, apart from the alluvial strath of the Naver, the interior consists of an undulating plateau of moorland and dreary monotonous peat bogs wherein numerous lochans are to be found. This uniformity of desolation is relieved by rocky outcrops of gneiss, particularly towards the coast.

The climate of the region is rigorous. The summers are short and cold (the mean July temperature is 55°F. , while the annual mean is 46°F.) but this is compensated for by the long hours of daylight.

The area is comparatively dry, the annual precipitation averaging 36 inches, fairly evenly distributed throughout the year. Wind is a major factor. It blows continuously, mainly from the north, occasionally attaining velocities of 100 m.p.h. As a result, great quantities of sand are blown inshore, piling against the cliffs, forming dunes, while further inland a machair develops. A further factor which affects the vegetation is the high latitude, many arctic-alpine species being found at sea level. The coastal region has a crofter population who rear sheep on the poor grassland and cultivate the more level tracts.

While there are few rare plants in the region, there blooms during the short spring and summer a rich profusion of those already well known. The species observed are recorded as they occur in communities.

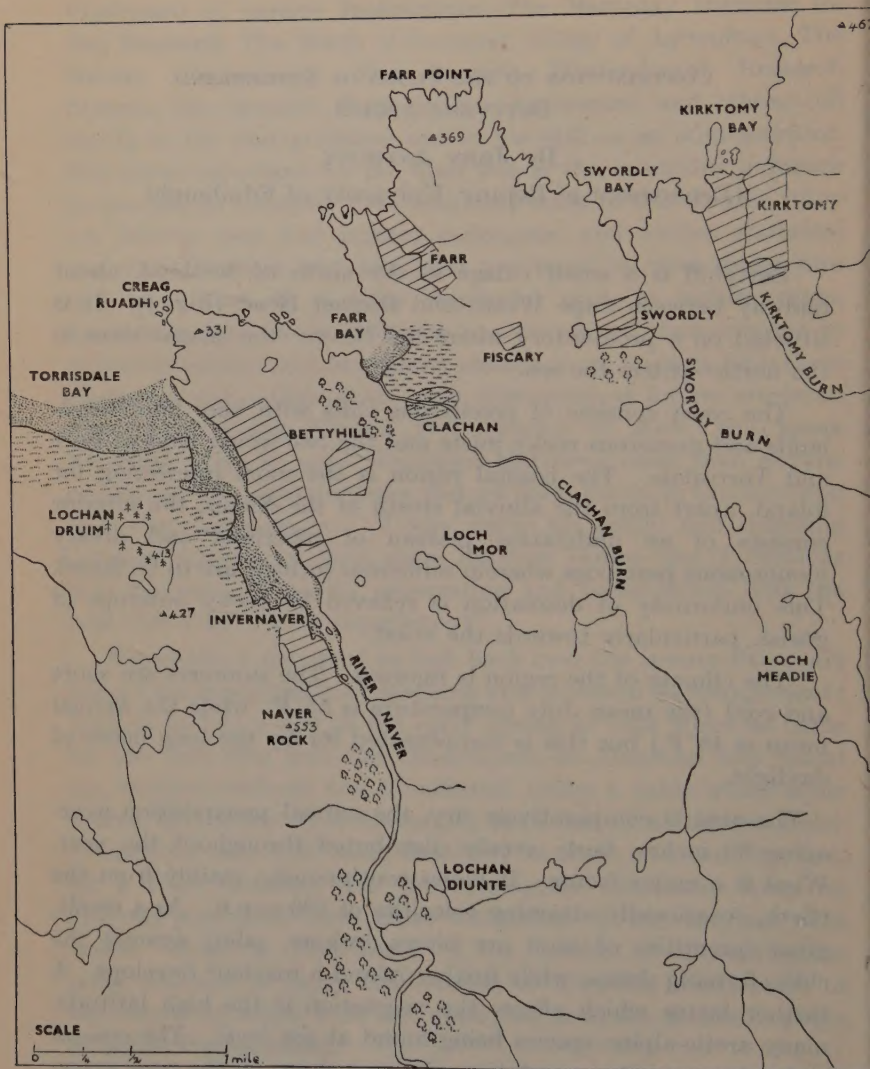


Fig. 1. BETTYHILL

COASTAL COMMUNITIES.

CLIFFS.

The coast consists of precipitous cliffs with scanty vegetation, but in sheltered inlets the rock ledges bear the following species:—

SILENE MARITIMA With.	ARMERIA MARITIMA Willd.
SAGINA MARITIMA Sm.	PLANTAGO MARITIMA L.
SEDUM ROSEA Scop.	PLANTAGO CORONOPUS L.
SEDUM ANGLICUM Huds.	MATRICARIA MARITIMA L.
LIGUSTICUM SCOTICUM L.	ASPLENIUM MARINUM L.

At Swordly and Kirtomy where the inlets provide a beach composed of large boulders and shingle, these species are to be found on the strand:—

COCHLEARIA SCOTICA Druce.	PLANTAGO MARITIMA L.
HONKEYNA PELOIDES Ehrh.	SONCHUS ARVENSIS L.
SPERGULARIA RUBRA J. & C.	MERTENSIA MARITIMA S. F. Gray.
Presl.	TRIGLOCHIN MARITIMA L.
RUMEX CRISPUS L.	CLAYTONIA ALSINOIDES Sims.
LIGUSTICUM SCOTICUM L.	

Along the cliff tops, where a short turf forms, *Primula scotica* Hook. grows in great profusion. *Oxyria digyna* L. and *Saxifraga oppositifolia* L. inhabit sheltered ravines of rivulets where they plunge over the cliff edge to the sea. Here and there on drier slopes *Vicia sylvatica* L. grows. On steep grassy slopes where the rocks are covered with soil, the maritime plants grow alongside those of the moorland, marsh, and weeds of cultivation such as:—

COCHLEARIA OFFICINALIS L.	URTICA DIOICA L.
PRUNELLA VULGARIS L.	HOLCUS LANATUS L.
ANGELICA SYLVESTRIS L.	PARNASSIA PALUSTRIS L.
ANTHYLLIS VULNERARIA L.	DACTYLIS GLOMERATA L.
PLANTAGO MARITIMA L.	RUMEX ACETOSELLA L.

On the sandy bay at Farr there is a zone of *Atriplex glabriuscula* Edm. and a few plants of *Cakile maritima* Scop. just below the high escarpment which bounds the dunes.

DUNES.

Dune land occurs at Farr Bay and begins at the beach where the sand forms a steep bank some twelve to fifteen feet high. Beyond this is an undulating area of fixed dune, but on the hillside to the east of the bay there is continuous wind erosion, giving rise to areas of bare sand. On the windward slopes the only two

species growing were *Oxytropis halleri* Bunge and *Ranunculus bulbosus* L.—persisting in this exposed position owing to their deep root systems. A curious alien, *Euphorbia cyparissias* L., is conspicuous, forming a large circular area on the grassy dunes. On the hillside above, it is found in amongst bracken which has colonised the leeward side of the hill.

To the west of the Naver there is a wide break in the cliffs, giving rise to the large Bay of Torrisdale. With greater exposure the seaward side of the hills is covered with loose sand and bears little or no vegetation. Further inland, the northern slopes of the Naver Rock are covered almost exclusively by *Dryas octopetala* L., which, owing to erosion, now forms large cushions some three to five feet in diameter. This formation extends up to an elevation of 100 feet where the *Dryas* thins out and merges into moorland vegetation. The following species were noted:—

THALICTRUM ARENARIUM Clap.	ARTEMISIA VULGARIS L.
RANUNCULUS ACRIS L.	ARCTIUM LAPPA L.
R. BULBOSUS L.	CIRSIIUM ARVENSE Scop.
EROPHILA VERNA Chevall.	C. VULGARE Ten.
VIOLA CANINA L.	HYPOCHAERIS RADICATA L.
POLYGALA VULGARIS L.	TRAGOPOGON PRATENSE L.
CERASTIUM ARVENSE L.	TARAXACUM OFFICINALE L.
C. VULGATUM L.	HIERACIUM PILOSELLA L.
C. SEMIDECANDRUM L.	LEONTODON HISPIDUS L.
C. TETRANDRUM Curt.	L. AUTUMNALIS L.
SAGINA NODOSA Fenzl.	CREPIS CAPILLARIS Wallr.
ARENARIA SERPYLLIFOLIA L.	SONCHUS OLERACEUS L.
A. LEPTOCLADOS Guss.	CAREX ARENARIA L.
STELLARIA MEDIA Vill.	C. MARITIMA Gunn.
LINUM CATHARTICUM L.	C. FLACCA Schreb.
GERANIUM MOLLE L.	FESTUCA RUBRA L.
ONONIS REPENS L.	POA PRATENSIS L.
MEDICAGO LUPULINA L.	P. TRIVIALIS L.
TRIFOLIUM REPENS L.	BROMIS MOLLIS L.
T. CAMPESTRE Schreb.	SEDUM ACRE L.
ANTHYLLIS VULNERARIA L.	SAXIFRAGA AIZOIDES L.
LOTUS CORNICULATUS L.	S. TRIDACTYLITES L.
VICIA CRACCA L.	PIMPINELLA SAXIFRAGA L.
V. SEPIUM L.	HERACLEUM SPHONDYLIIUM L.
LATHYRUS PRATENSIS L.	DAUCUS CAROTA L.
POTENTILLA ANSERINA L.	CENTAUREA NIGRA L.
GALIUM VERUM L.	C. SCABIOSA L.
SENECIO JACOBÆA L.	VERONICA AGRESTIS L.
BELLIS PERENNIS L.	EUPHRASIA BREVIPILA B. & G.
ACHILLEA MILLEFOLIUM L.	THYMUS DRUCEI Ronn.
CHRYSANTHEMUM LEUCANTHEMUM L.	PLANTAGO LANCEOLATA L.

P. MARITIMA L.	AIRA PRAECOX L.
AGROPYRON JUNCIFORME A. & D.	A. CARYOPHYLLEA L.
Love.	DACTYLIS GLOMERATA L.
A. REPENS Beauv.	AMMOPHILA ARENARIA Link.
HELICOTRICHON PUBESCENS	AGROSTIS STOLONIFERA L.
Pilger.	LOLIUM PERENNE L.

MACHAIR.

A wide area of machair extends eastwards of Farr Bay from the cliffs overlooking the sand-dunes to Fiscary and Farr. On the rocky outcrops *Oxytropis halleri* Bunge is abundant and *Draba incana* L. common, while *Scilla verna* Huds. is ubiquitous on the sward above the rocks. The area is undulating and a striking feature is that the summits of the knolls are densely covered with *Dryas octopetala*. Other species present are:—

TROLLIUS EUROPAEUS L.	THYMUS DRUCEI Ronn.
THALICTRUM ARENARIUM Clap.	PLANTAGO MARITIMA L.
POLYGALA VULGARIS L.	CAMPANULA ROTUNDIFOLIA L.
P. OXYPTERA Rchb.	GALIUM VERUM L.
TRIFOLIUM PRATENSE L.	ACHILLEA MILLEFOLIUM L.
T. MEDIUM Huds.	ANTENNARIA DIOICA Gaertn.
T. REPENS L.	LUZULA MULTIFLORA Lej.
BELLIS PERENNIS L.	EPIPACTIS ATRO-RUBENS Schultes.
SENECIO JACOBAEA L.	LISTERA OVATA R. Br.
TARAXACUM OFFICINALE L.	GYMNADENIA CONOPSEA R. Br.
LEONTODON AUTUMNALIS L.	COELOGLOSSUM VIRIDE Hartm.
L. HISPIDUS L.	ORCHIS FUCHSII Druce.
HIERACIUM PILOSELLA L.	O. MASCULA L.
LUZULA CAMPESTRIS DC.	CAREX ARENARIA L.
ANTHYLLIS VULNERARIA L.	C. NIGRA Reich.
SALIX REPENS L.	C. OVALIS Good.
DAUCUS CAROTA L.	CYNOSURUS CRISTATUS L.
PIMPINELLA SAXIFRAGA L.	KOELERIA GRACILIS Pers.
POLYGONUM VIVIPARUM L.	FESTUCA RUBRA L.
PRIMULA VERIS L.	F. VIVIPARA Sm.
GENTIANELLA CAMPESTRIS Sm.	AIRA CARYOPHYLLEA L.
G. SEPTENTRIONALIS E. F. W.	EQUISETUM ARVENSE L.
EUPHRASIA spp.	SELAGINELLA SELAGINOIDES Link.
PRUNELLA VULGARIS L.	BOTRYCHIUM LUNARIA Sw.

MOORLAND.

By far the greater part of the region is covered by moorland which comprises a wide range of habitats from dry grassy heath to wet peat bogs which bear these species:—

POLYGALA SERPYLLIFOLIA Hose.	HYPERICUM PULCHRUM L.
CERASTIUM VULGATUM L.	LINUM CATHARTICUM L.

ULEX EUROPAEUS L.	NARTHECIUM OSSIFRAGUM Huds.
JUNCUS SQUARROSUS L.	SCHOENUS NIGRICANS L.
LUZULA MULTIFLORA Lej.	RHYNCHOSPORA ALBA Vahl.
ORCHIS MASCULA L.	CAREX BINERVIS Sm.
O. ERICETORUM E. R. L.	C. DISTICHA Huds.
O. PURPURELLA T. & T. A. Steph.	C. DEMISSA Hornem.
ELEOCHARIS PALUSTRIS R.Br.	C. ECHINATA Murr.
LATHYRUS MONTANUS Bernh.	C. HOSTIANA DC.
POTENTILLA ERECTA Rausch.	C. NIGRA Reich.
SAXIFRAGA AIZOIDES L.	C. PILULIFERA L.
S. OPPOSITIFOLIA L.	C. PULICARIS L.
DROSER A ANGLICA Huds.	C. ROSTRATA Stokes.
D. ROTUNDIFOLIA L.	C. CAPILLARIS L.
RUMEX ACETOSELLA L.	C. DIOICA L.
R. ACETOSA L.	C. FLACCA Schreb.
SALIX REPENS L.	C. LEPIDOCARPA Tausch.
ERICA TETRALIX L.	C. PAUCIFLORA Lightf.
E. CINEREA L.	EMPETRUM NIGRUM L.
ARCTOSTAPHYLOS UVA-URSI Spreng.	AGROSTIS CANINA L.
CALLUNA VULGARIS Hull.	A. TENUIS Sibth.
MELAMPYRUM PRATENSE L.	DESCHAMPSIA FLEXUOSA Trin.
EUPHRASIA spp.	FESTUCA OVINA L.
VERONICA SERPYLLIFOLIA L.	MOLINIA COERULEA Moench.
PINGUICULA LUSITANICA L.	NARDUS STRICTA L.
P. VULGARIS L.	SIEGLINGIA DECUMBENS Bernh.
GALIUM HERCYNICUM Weigel.	LYCOPodium SELAGO L.
SUCCISA PRATENSIS Moench.	

MARSHES.

Marshes occur in the low-lying flats bordering streams. These species are common:—

CALTHA PALUSTRIS L.	ANAGALLIS TENELLA Murr.
RANUNCULUS FLAMMULA L.	MYOSOTIS PALUSTRIS L.
R. HEDERACEUS L.	M. SECUNDA Murr.
RHINANTHUS MINOR Ehrh.	M. CAESPITOSA Schultz.
R. STENOPHYLLUS Druce.	SCROPHULARIA NODOSA L.
MENTHA AQUATICA L.	MIMULUS GUTTATUS DC.
SENECIO AQUATICUS Hill.	PEDICULARIS PALUSTRIS L.
CARDAMINE PRATENSIS L.	P. SYLVATICA L.
NASTURTIUM OFFICINALE R.Br.	GALIUM PALUSTRE L.
N. MICROPHYLLUM Reich.	ACHILLEA PTARMICA L.
VIOLA PALUSTRIS L.	CIRSIUM PALUSTRE Scop.
LYCHNIS FLOS-CUCULI L.	ODONTITIS VERNA Dum.
MONTIA FONTANA L.	GALIUM HERCYNICUM Weigel.
PARNASSIA PALUSTRIS L.	SUCCISA PRATENSIS Moench.
EPILOBIUM MONTANUM L.	TRIGLOCHIN PALUSTRIS L.
CALLITRICHE STAGNALIS Scop.	POTAMOGETON POLYGONIFOLIUS Pourr.
HYDROCOTYLE VULGARIS L.	NARTHECIUM OSSIFRAGUM Huds.
MYRICA GALE L.	JUNCUS SQUARROSUS L.

J. BUFONIUS L.
 J. EFFUSUS L.
 J. CONGLOMERATUS L.
 J. BALTICUS Willd.
 J. ARTICULATUS L.
 J. ACUTIFLORUS Hoffm.
 J. KOCHII Schultz.

J. BULBOSUS L.
 ERIOPHORUM ANGUSTIFOLIUM Honck.
 IRIS PSEUDACORUS L.
 BLYSMUS RUFUS Link.
 PHRAGMITES COMMUNIS Trin.
 PHALARIS ARUNDINACEA L.

LOCHANS.

Lying in hollows in the moorland are numerous lochans, some of which are fringed with marshland bearing a rich flora, while in others peat bog extends to their shores.

RANUNCULUS FLAMMULA L.	PEDICULARIS PALUSTRIS L.
CALTHA PALUSTRIS L.	UTRICULARIA INTERMEDIA Hayne
NYMPHAEA ALBA L.	LITTORELLA UNIFLORA Aschers.
POTENTILLA PALUSTRIS Scop.	LOBELIA DORTMANNA L.
EPILOBIUM PALUSTRE L.	POTAMOGETON NATANS L.
MYRIOPHYLLUM ALTERNIFOLIUM DC.	SCHOENOPLECTUS LACUSTRIS Palla.
POLYGONUM AMPHIBIUM L.	ELEGITON FLUITANS Link.
MENYANTHES TRIFOLIATA L.	CAREX VESICARIA L.
MYOSOTIS CAESPITOSA Schultz.	GLYCERIA FLUITANS R.Br.
VERONICA SCUTELLATA L.	PHRAGMITES COMMUNIS Trin.
V. BECCABUNGA L.	EQUISETUM FLUVIATILE L.

WOODLANDS.

Owing to the exposed nature of the terrain, natural woodland is scanty. It is to be found in situations sheltered from the wind, occurring as scattered clumps in the haughlands of Strathnaver, while a small wood is found at Farr Bay and another at Swordly.

The trees comprise principally birch (*B. pubescens* and occasionally *B. verrucosa*), rowan, hazel, willows (*S. aurita* and *S. atrocinerea*), while in Strathnaver along the watercourses alder flourishes. At Farr Bay *Prunus spinosa* forms a protective outer barrier.

Woody species also occur in the ravines cut by the numerous streams as they descend from the interior plateau to the sea. In these on wind-swept ledges stunted aspen and holly cling.

The ground flora of these woods contains the following species:—

RANUNCULUS FICARIA L.	S. GRAMINEA L.
CARDAMINE FLEXUOSA With.	MOEHRINGIA TRINERVIA Clairv.
C. HIRSUTA L.	ULEX EUROPAEUS L.
VIOLA RIVINIANA Rehb.	GERANIUM ROBERTIANUM L.
HYPERICUM PULCHRUM L.	OXALIS ACETOSELLA L.
STELLARIA HOLOSTEA L.	ALCHEMILLA FILICAULIS Buser.

A. GLABRA Neyg.	LONICERA PERICLYMENUM L.
A. XANTHOCHLORA Rothm.	VALERIANA OFFICINALIS
FRAGARIA VESCA L.	SOLIDAGO VIRGAUREA L.
GEUM RIVALE L.	CIRSIIUM HETEROPHYLLUM Hill.
ROSA CANINA L.	ALLIUM URSINUM L.
R. SPINOSISSIMA L.	LUZULA PILOSA Willd.
RUBUS SAXATILIS L.	L. SYLVATICA Gaud.
CHRYSOSPLENIUM OPPOSITIFOLIUM L.	BRACHYPODIUM SYLVATICUM Beauv.
HEDERA HELIX L.	DESCHAMPSIA CAESPITOSA Beauv.
SANICULA EUROPAEA L.	PTERIDIUM AQUILINUM Kuhn.
CONOPODIUM MAJUS Lor. & Barr.	ASPENIUM ADIANTUM-NIGRUM L.
ANGELICA SYLVESTRIS L.	ATHYRIUM FILIX-FEMINA Roth.
VACCINIUM MYRTILLUS L.	CYSTOPTERIS FRAGILIS Bernh.
EMPETRUM HERMAPHRODITUM Hag.	DRYOPTERIS FILIX-MAS Schott.
LYSIMACHIA NEMORUM L.	D. BORRERI Newn.
PRIMULA VULGARIS Huds.	D. AUSTRIACA Woyner.
DIGITALIS PURPUREA L.	THELYPTERIS PHEGopteris Sloss.
VERONICA OFFICINALIS L.	T. OREOPTERIS C. Chr.
STACHYS SYLVATICA L.	T. DRYOPTERIS Sloss.
S. PALUSTRIS L.	BLECHNUM SPICANT Roth.
STACHYS × AMBIGUA Sm.	POLYSTICHUM LONCHITIS Roth.
TEUCRIUM SCORODONIA L.	POLYPODIUM VULGARE L.
AJUGA PYRAMIDALIS L.	EQUISETUM SYLVATICUM L.

A different type of woodland occurs on the high ground to the west of the Naver. Here on the south-facing slopes of the hill a wide area is dominated by *Juniperus communis* L. which grows to a height of from one to three feet. On the rocky outcrops *Empetrum nigrum* L. and *Arctostaphylos uva-ursi* are abundant, while *Salix repens* spreads on the drier area. To the south of Loch Drumm on the north-facing slopes, the rocky ledges are covered with *Dryas octopetala* L. *Asplenium trichomanes* L., *A. ruta-muraria* L., *A. adiantum-nigrum* L. and *Cystopteris fragilis* Bernh. are common in the rock crevices.

CULTIVATED GROUND.

Only a small proportion of the ground is cultivated and this is located near the sea where the soil is affected by blown sand—at Bettyhill, Farr and Kirtomy. In Strathnaver where there is good land, the soil is a mixture of sand, gravel and peat. The chief crops are hay, oats and potatoes. Most crops bear a high proportion of weeds, among which the following species were noted:—

RANUNCULUS ACRIS L.	SINAPIS ARVENSIS L.
R. REPENS L.	SISYMBRIUM OFFICINALE Scop.
FUMARIA OFFICINALIS L.	CAPELLA BURSA-PASTORIS L.

- VIOLA TRICOLOR L.
MELANDRIUM RUBRUM Garcke.
M. ALBUM Garcke.
CERASTIUM VULGATUM L.
STELLARIA MEDIA Vill.
SAGINA PROCUMBENS L.
SPERGULA ARVENSIS L.
CHENOPODIUM ALBUM L.
TRIFOLIUM PRATENSE L.
T. DUBIUM Sibth.
LYCOPSIS ARVENSIS L.
MYOSOTIS ARVENSIS Hill.
VERONICA CHAMAEDRYIS L.
EUPHRASIA OFFICINALIS L.
ODONTITES VERNIA Dum.
RHINANTHUS MINOR L.
LAMIAM PURPUREUM L.
GALEOPSIS TETRAHIT L.
PLANTAGO MAJOR L.
GALIAM APARINE L.
KNAUTIA ARVENSIS Coult.
SENECIO VULGARIS L.
TUSSILAGO FARFARA L.
GNAPHALIAM SYLVATICUM L.
MATRICARIA MATRICARIOIDES Port.
CHRYSANTHEMUM SEGETUM L.
C. PARTHENIUM Bernh.
- VICIA CRACCA L.
V. SEPIUM L.
LATHYRUS PRATENSIS L.
ANTHRISCUS SYLVESTRIS Bernh.
HERACLEUM SPHONDYLIIUM L.
EUPHORBIA HELIOSCOPIA L.
RUMEX ACETOSELLA L.
R. ACETOSA L.
R. OBTUSIFOLIUS L.
POLYGONUM AVICULARE L.
P. PERSICARIA L.
URTICA DIOICA L.
SONCHUS OLERACEUS L.
LAPSANA COMMUNIS L.
CIRSIIUM ARVENSE Scop.
C. VULGARE Ten.
CENTAUREA SCABIOSA L.
C. NIGRA L.
DACTYLIS GLOMERATA L.
AGROPYRON REPENS Beauv.
ARRHENATHERUM ELATIUS J. & C.
Presl.
HOLCUS LANATUS L.
ALOPECURUS PRATENSIS L.
PHELIUM PRATENSE L.
LOLIUM PERENNE L.

THE MYCORRHIZA OF ORCHIS PURPURELLA.

By D. G. DOWNIE

(Department of Botany, University of Aberdeen).

Orchis purpurella T. & T. A. Steph., a widely distributed marsh orchid in Scotland, was examined for its associated mycorrhizal fungus. Plants were obtained from three dispersed areas in the vicinity of Aberdeen. The roots of all plants showed normal infection. Adopting the accepted procedure of plating sections of surface-sterilised whole roots, many distinct endophytes were isolated but all were species of *Rhizoctonia*. In general all the roots of any one plant yielded the same fungus but the isolates derived from different plants varied in colour, growth rate, hyphal diameter and sclerotial formation. The orchid is thus non-specific with regard to its symbiont and proof of this was established by seed germination tests under controlled conditions. All the isolates proved true symbionts stimulating the growth of the embryos but, within the limits of the experiment, the degree of stimulation varied with the form of fungus. The effect of the symbiont was gauged by the average size of protocorms after seven weeks growth at 20° C. on comparable media, but the diversity in growth attained in that time may reflect differences in growth rate of the introduced fungi rather than their proficiency as symbionts. In this connection it had been observed that the parent plants from which distinct isolates were obtained had all been noted as equally robust, so that, assuming that the growing plant derives benefit from the associated fungus, one might argue that the varied symbionts are equally effective. On the other hand the plants are perennial; a new crop of roots is formed towards the end of the growing season and it is those roots which yield the fungi isolated the following June. The fungus partner of any one season may therefore differ from that of the previous season and the assessment of the vigour of the adult on the associated fungus of the current year might not be essentially valid.

The fungus most frequently isolated was the sterile form of *Corticium solani* (Prill. & Delacr.), Bourd. & Galz, *Rhizoctonia solani* Kühn. (syn. *Pellicularia filamentosa* (Pat.) Rogers), a

widespread soil-inhabiting fungus, strains of which are pathogenic on a variety of hosts. In culture with the seed of *O. purpurella* it acts as a symbiont—host cells are penetrated, hyphal pelotons are formed, digestion of the filaments takes place and the growth of the embryos is greatly stimulated—it has, indeed, all the characteristics of an orchid mycorrhizal fungus. The pathogenicity of the strains isolated from the orchid has not been tested but pathogenic strains of the fungus from different hosts obtained outwith the laboratory have proved acceptable mycorrhizal associates of *O. purpurella*. It is of interest to note that on the sheath and reduced blade of a basal leaf of one plant of *O. purpurella* a tenuous fructification of the *Corticium* type was found. A systematic search for fructifications on other plants of the orchid was unsuccessful. The one fructification was immature, but, as far as comparisons could be made, it appeared almost identical with that of *C. solani* on the stems of potato.

The following is an account of the *Rhizoctonia* spp. isolated from *O. purpurella* and their relative effects on seed germination under controlled conditions. Experimental evidence that pathogenic and saprophytic strains of *C. solani* are acceptable symbionts is given. Comparative growth studies of the protocorms developed with orchid endophytes and with strains of *C. solani* from other hosts are also presented. In the discussion advantage is taken of the considerable data accumulated for the plant pathogen *R. solani*—symbiont of *O. purpurella*—to reassess the morphology and ecology of the lesser known orchid endophytes in the *Rhizoctonia* group.

ENDOPHYTES OF *O. PURPURELLA*.

Two plants of *O. purpurella* brought into the laboratory on separate occasions yielded different *Rhizoctonia* isolates both capable of stimulating embryo development. One of these isolates was identified as *R. solani* and a systematic study was undertaken to determine whether this widespread soil fungus was a frequent symbiont of the orchid. Fourteen plants from three areas—Scotstoun Moor, Grandholme Moss and Newburgh Dunes—were examined. The plants were designated by letters and descriptive notes were made of each specimen. All the roots of each plant were surface-sterilised with 0.1% HgCl_2 for two minutes, washed in sterile water and cut aseptically into 2-3 mm. segments, the

segments of any one root being plated separately on potato dextrose agar. Fungi were extracted successfully from eight plants, bacterial contamination of the plates accounting for the failure in other instances. The many isolates from each plant were numbered consecutively. On examination it was found that the isolates from all the roots of any one plant were similar, therefore only eight isolates were retained in stock, one from each plant. The endophytes were all forms of the genus *Rhizoctonia*.

To study the variation in vegetative character, comparable cultures of isolates were made following the method of Flentje (1956). All were grown on potato dextrose marmite agar and incubated at 25° C. After 3 days, 5 mm. discs were cut from the margin of the colonies, transferred to fresh P.D.M.A. and again incubated at 25° C. The hyphae measured were taken from 1 cm. segments at the margin of a new colony after 3 days, in the case of the fast growing forms, and after the slower growing forms had developed a colony equal in diameter to that of fast growing ones (5-7 days). Growth rate was determined from 2nd-4th day while hyphal and sclerotial colour, type of sclerotial formation, and size of sclerotial cells were noted after 3-4 weeks growth of the colonies.

Table I gives the locality of the various plants and summarises the characters of their endophytes.

Three groups were recognised: (a) forms which developed brown hyphae, cylindrical oidial cells and brown sclerotia (B.12, C.1, J.16, L.10); (b) forms with white slender hyphae, ovoid almost globular, oidial cells, and without defined sclerotia (A.33, D.5, H.13); (c) an isolate with cream coloured slender hyphae, cylindrical oidial cells, and without defined sclerotia (E.1). The forms in each group were alike morphologically but the variation between the groups appeared to be of specific rank. Three species of *Rhizoctonia* are therefore recognised as endophytes of *O. purpurella*: *R. solani*, Kühn (a), *R. repens*, Bernard (b) and a third unidentified species (c). *R. solani* was isolated from plants growing in two distinct soil types (moor and sand dune) in widely separated localities and from four of the eight plants examined. Thus it appears to be frequently present as an endophyte of this orchid. All three species occurred in the roots of adult plants but seed germination tests are necessary before the status of these fungi as symbionts can be evaluated. All isolates were

TABLE I—ENDOPHYTES.

Plant	Locality	Isolate	Colour of mycelium	Diam. in μ , of the hyphae	Nuclear condition of cells	Sclerotia	Shape of sclerotial cell	Size of sclerotial cell in μ .	Growth-rate mm./hr.
A	Scotstoun	A.83	white	4.5-6	binucleate	not defined	ovoid	12-18 $\times$ 10-15	0.13
B	"	B.12	brown	7.8-5	multi-nucleate	dark brown scattered	cylindrical	35-70 $\times$ 17-23	0.50
C	"	C.1	pale brown	7.9-5	"	light brown scattered	"	26-75 $\times$ 12-18	0.58
D	"	D.5	white	4.5	binucleate	not defined	ovoid	14-17 $\times$ 10-14	0.11
E	"	E.1	cream	4.5-6	"	"	cylindrical	27-50 $\times$ 8-11	0.35
H	Grandholme	H.13	white	4.5	"	"	ovoid	13-19 $\times$ 12-18	0.15
J	Newburgh	J.16	brown	8-10	multi-nucleate	dark brown crusted	cylindrical	27-65 $\times$ 13-18	0.54
L	"	L.10	brown	8-10	"	"	"	28-72 $\times$ 14-19	0.54

subjected to the tests, but, as J.16 and L.10 were similar morphologically and not demonstrably different in measurement statistically, J.16 was omitted from the experiment.

GERMINATION TESTS.

The method used in all germination tests was similar to that described for other terrestrial orchids (Downie, 1940). All experimental tubes were incubated in darkness at 20° C. for a period of seven weeks. The test media at first used were distilled water agar and Pfeffer + 1% dextrose agar. In later experiments these two media were replaced by Pfeffer + 1% potato starch agar. On all three media the embryos develop until the seed coats are ruptured but in the absence of a symbiont, growth ceases after the protocorms have reached a length of 200-250 μ . Unlike many other orchids (*Goodyera repens*, *Listera cordata*, etc.) soluble carbohydrate in the form of dextrose (0.5-2%) does not stimulate further growth. The change from sugar to starch in the experimental media was the result of preliminary germination tests with strains of *Rhizoctonia solani*. It was found that a greater number of strains of this fungus reacted as successful symbionts when the carbohydrate source was starch and the change did not reflect on the development of the embryos induced by other species of *Rhizoctonia*. In Table II (below) growth responses of the embryos with the varied isolates extracted from the roots of adult plants of *O. purpurella* are given. The numbers quoted represent the average length and breadth in μ of one hundred protocorms taken at random from the culture tubes. The experimental medium was Pfeffer's mineral salts + 1% potato starch + 1.5% agar and the duration of the experiment seven weeks at 20° C.

TABLE II.

Control		Endophytes of <i>Orchis purpurella</i>						
None		A.33	B.12	C.1	D.5	E.1	H.13	L.10
Length	243	598	1240	1175	593	1178	488	1280
	x	x	x	x	x	x	x	x
Breadth	177	376	733	729	345	828	320	888

It will be noted that all endophytes stimulated growth of the embryos beyond that of the control. Endophytes identified as *R. repens* (A.33, D.5, H.13) were much less effective than either those of the *R. solani* group (B.12, C.1, L.10) or *Rhizoctonia*

sp. (E.1). The differential response of the embryos, observed above, could be correlated with the relative growth-rate of the respective endophytes if only the two species *R. repens* (av. growth-rate 0.13 mm./hr.) and *R. solani* (av. growth-rate 0.54 mm./hr.) were considered, i.e. the faster growing endophyte stimulating more rapid growth of the embryos. On the other hand, *Rhizoctonia* sp. (E.1) has a growth-rate (0.35 mm./hr.) substantially less than any of the forms of *R. solani*, yet the stimulation of the embryos by both species is almost identical. The growth-rate of the associated fungus cannot therefore be upheld as the only effective variant in embryo stimulation. Symbiotic seedlings would have to be maintained for a very much longer period before the relative efficiency of the different endophytes could be ascertained.

Species of *Rhizoctonia* with white or cream-coloured mycelium, varying in hyphal diameter, shape of sclerotial or oidial cell and degree of sclerotial development as in A.33, D.5, E.1 and H.13, are frequently isolated from terrestrial orchids but heretofore I had never encountered an endophyte which developed brown hyphae and dark-brown sclerotia of the encrusted or knot-formation type. Interest therefore centred round isolates B.12, C.1 and L.10 which, though differing from each other in mycelial colour and sclerotial formation have the morphological characteristics and hyphal measurements of *R. solani* Kuhn. Table II shows that the varying forms of this species are effective symbionts of *O. purpurella* giving a growth stimulus to the embryo equalled only by one other species of *Rhizoctonia* (E.1).

The forms of *R. solani* (B.12, C.1, L.10) used in the above germination tests were symbionts of the orchid and their status as saphrophytes or potential parasites was unknown. In the next series of germination experiments, known pathogenic strains (from tomato, cauliflower and wheat) and forms from the surface of potato tubers were introduced into the culture tubes to test their ability as mycorrhizal fungi. The strain from wheat (Cs1) was obtained from the Commonwealth Mycological Institute and was originally isolated by Dr. Mary Glynne from affected wheat while that from cauliflower (Rs5) was obtained by courtesy of Mr. A. Channon from the National Vegetable Research Station, Wellesbourne. All other strains were isolated in this laboratory.

TABLE III—RHIZOCTONIA SOLANI.

Strain Number	Origin	Colour of mycelium	Diam. in μ . of the hyphae	Nuclear condition of cells	Sclerotia	Shape of sclerotial cell	Size of sclerotial cell in μ .	Growth-rate mm./hr.
Rs1	Tomato	pale brown	7-10.5	Multi-nucleate	brown-scattered	cylindrical ovoid	21-62 $\times$ 13-19	0.46
Rs4	Potato	brown	7-11	"	brown-encrusted	cylindrical	25-63 $\times$ 10-15	0.50
Rs5	Cauliflower	cream	7.5-10.5	"	brown-scattered small	"	30-45 $\times$ 10-15	0.42
Rs6	Potato—Kerr's Pink	fawn	8.5-11.5	"	brown-small massed	"	25-73 $\times$ 10-20	0.67
Rs7	Potato—Majestic	light brown	7.5-9.5	"	brown-encrusted	"	30-76 $\times$ 11-18	0.50
Rs8	Potato—Brit. Queen	brown	9-11	"	brown-large massed	cylindrical ovoid	27-62 $\times$ 12-20	0.54
Cs1	Wheat	cream	3.5-5	binucleate	brown-scattered small	cylindrical	16-28 $\times$ 9-12	0.13

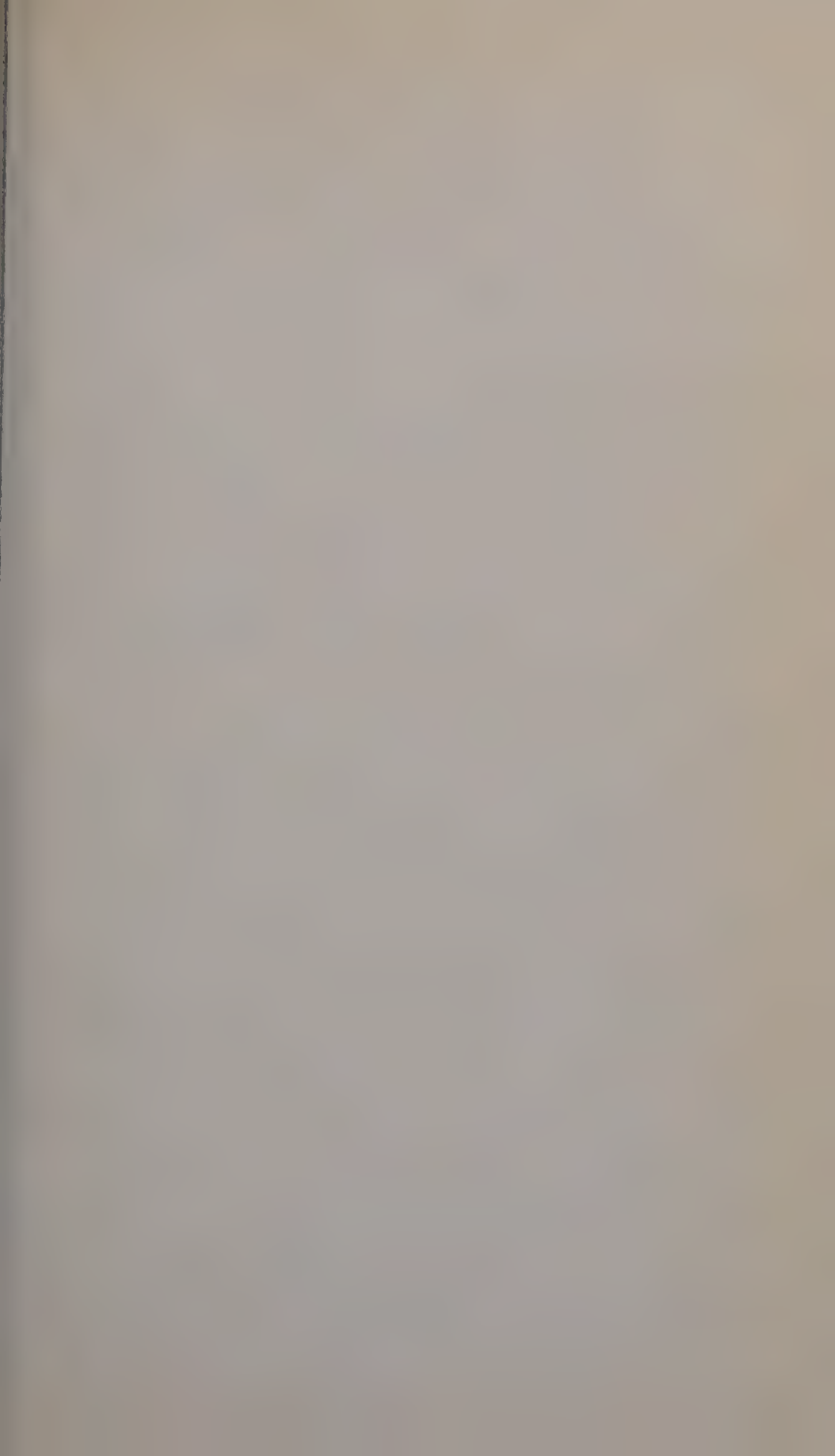
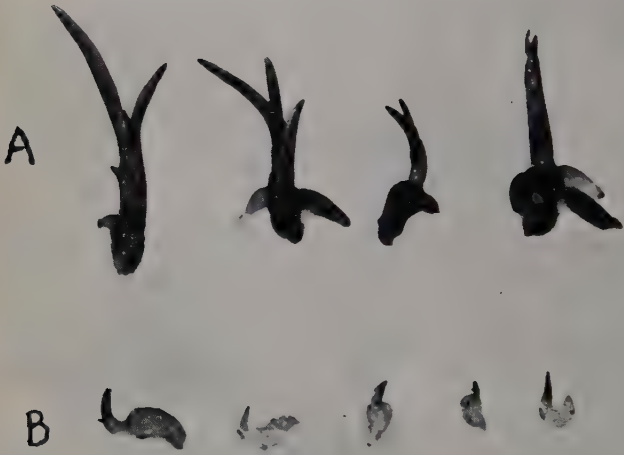


PLATE I



Seedlings of *O. purpurella* obtained from seed cultures inoculated with pathogenic strains of *C. solani*.

A—2 year old seedlings—symbiont *C. solani* (Cs1) from wheat.

B—1 year old seedlings—Symbiont *C. solani* (Rs5) from cauliflower.

As fructifications of the experimental strains have not been observed the name *R. solani* has been retained for all forms except the one from wheat which is listed as *C. solani* in the C.M.I. catalogue.

Table III gives the origin of the seven strains tested and their characteristic features as observed from comparable potato dextrose marmite cultures.

Table IV shows growth responses of the embryos of *O. purpurella* with forms of *R. solani* from hosts other than the orchid. The experimental conditions were similar to those described for the endophytes. The numbers quoted represent the average length and breadth in μ of 100 protocorms.

TABLE IV.

Control		Forms of <i>Rhizoctonia solani</i>						
None		Rs1	Rs4	Rs5	Rs6	Rs7	Rs8	Cs1
Length	243	952	282	331	1204	321	326	808
	x	x	x	x	x	x	x	x
Breadth	177	636	234	268	721	262	269	637

The growth response of the embryos which accept Rs1 (tomato), Rs6 (potato) and Cs1 (wheat) as symbionts is considerable but the other forms of the fungus are not equally effective. As the measurements show, the growth obtained with Rs4, 7 and 8 (potato) and Rs5 (cauliflower) is apparently little better than the control, yet this slight stimulation is not to be discounted since protocorms retained in culture and having Rs5 as a symbiont continued development, producing sturdy plantlets in twelve months as shown in Plate IB. The above experiments show that *R. solani* can act as a symbiont of *O. purpurella* and that strains, including pathogens, derived from other hosts are as effective as those isolated from the orchid.

STATISTICAL ANALYSIS OF EXPERIMENTAL FUNGI.

To study the variation in the dimensions of the fungi used experimentally, ten diameter measurements of runner hyphae, side branches and sclerotial cells were taken of each from comparable P.D.M.A. cultures. In addition and, as a point of interest, similar measurements of *R. goodyerae-repentis* (Gr.14) from *Goodyera repens* and *Rhizoctonia* sp. (Pb.1) from *Platanthera bifolia* were made and included in the analysis (Table V).

TABLE V.
STATISTICAL ANALYSIS OF EXPERIMENTAL FUNGI.
Totals of 10 diameters: measurements in μ .

	Fungus number	Species	Runner hyphae	Side hyphae	Sclerotial cells
Endophytes of <i>O. purpurella</i>	E.1	<i>Rhizoctonia</i> sp.	500	600	845
	A.33	„ <i>repens</i>	545	375	1190
	D.5	„ „	465	290	1165
	H.13	„ „	465	360	1405
	B.12	„ <i>solani</i>	750	875	1830
	C.1	„ „	780	875	1390
	J.16	„ „	895	850	1645
	L.10	„ „	820	835	1655
Strains of <i>Rhizoctonia solani</i>	Rs1	<i>Rhizoctonia solani</i>	925	870	1635
	Rs4	„ „	895	845	1135
	Rs5	„ „	980	805	1320
	Rs6	„ „	1000	887	1570
	Rs7	„ „	890	890	1455
	Rs8	„ „	990	855	1565
	Cs1	<i>Corticium solani</i>	440	655	965
	Gr14	<i>Rhizoctonia goodyerae-repentis</i>	455	750	1165
Endophytes of other orchids	Pb1	„ sp.	525	460	700
Least significant difference between any two totals ($P = 0.05$)			=67	71.5	159

The statistical analysis was disappointing in that it failed to assist in the classification of the varied forms of *R. solani*. Considerable variation in measurement was revealed even with forms derived from the same host (e.g. Rs4, 6, 7 and 8 from potato). On the other hand it was interesting to note that forms from the orchid (J.16, L.10) were not demonstrably different in measurement from the strain isolated from diseased tomatoes (Rs1). A statistical analysis of hyphal diameters of main and side branches in seven strains of *Pellicularia filamentosa* (Pat.) Rogers, [*Rhizoctonia solani* Kühn] was given by N. T. Flentje (1956). It was hoped that by adopting his cultural methods, comparable strains among his isolates and those used in the orchid experiments might be demonstrated. Unfortunately, as actual measurements are not quoted in his analysis, no comparison could be drawn.

The forms of *R. solani* used experimentally vary in colour of mycelium and sclerotial development but, with the exception of the one from wheat (Cs1), conform to a reasonable extent in measurement of hyphae and sclerotial cells. *C. solani* (Cs1) appears to be quite a distinct strain with finer hyphae and smaller sclerotial cells. The difference is further enhanced in the nuclear

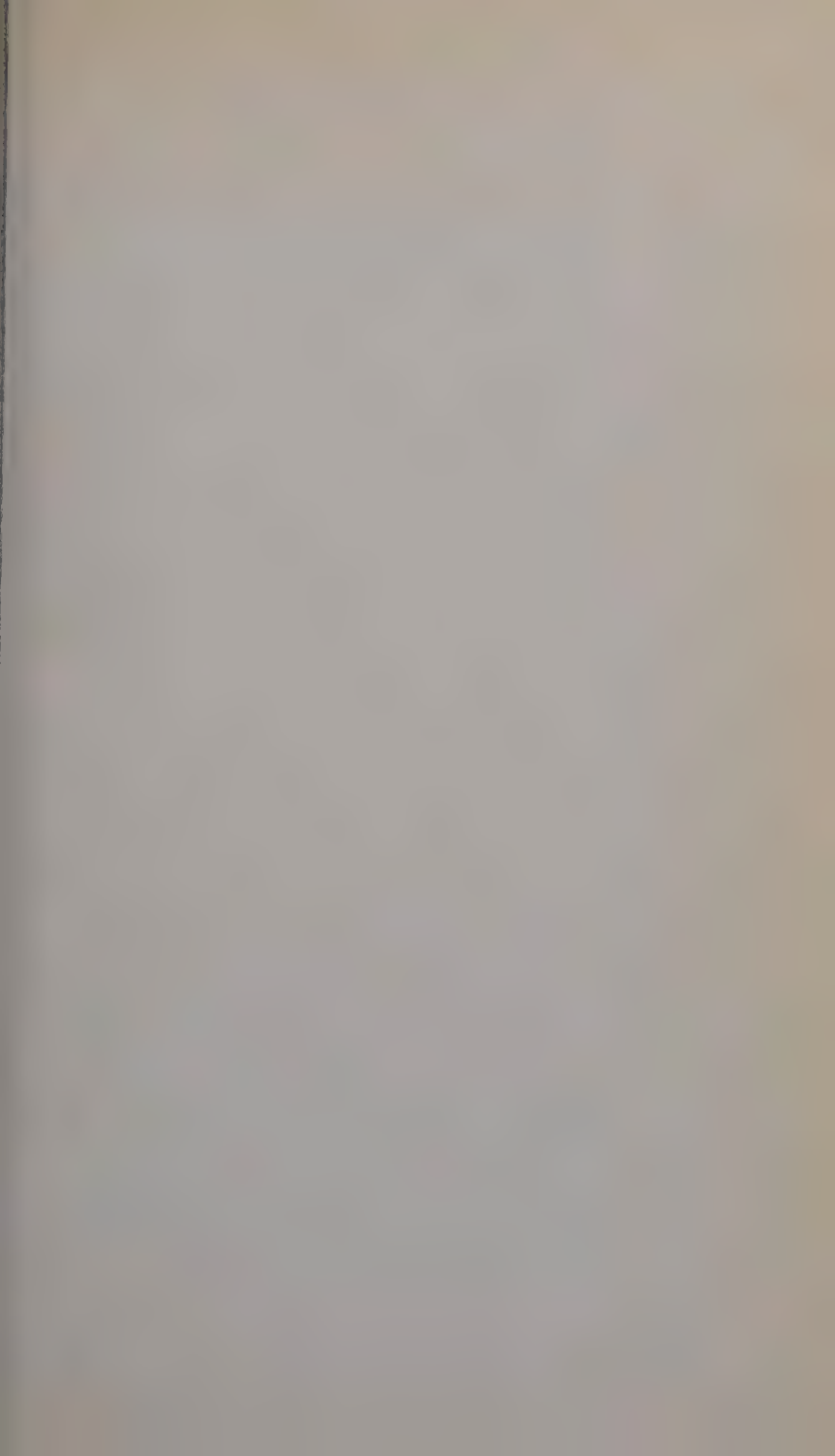


PLATE II



Fructification of *Corticium solani* on leaf sheaths and basal leaf of *Orchis purpurella*.

condition of the cells, as it alone is binucleate all other forms of *R. solani* being multinucleate. The nuclear condition was determined by staining thin films of the mycelium with basic fuchsin according to the method of De Lamater (1948) and was confirmed by fluorescent microscopy. While the multinucleate condition of the cells is an accepted feature of *R. solani*, all *Rhizoctonia* spp. isolated hitherto from orchids (*Goodyera repens*, *Platanthera bifolia*, *Listera ovata*, *L. cordata* and *Leucorchis albida*) have had prevailingly binucleate cells. It is of interest to note that a nuclear condition which prevails in orchid *Rhizoctonia* spp. can occur in a strain of *R. solani*. Taken in conjunction with the fact that the latter is an orchid endophyte a closer affinity may exist between orchid *Rhizoctonia* spp. and the very variable fungus *R. solani* than previously visualised. Further experiments are designed to test the reaction of *R. solani* with other orchid species, particularly those which are non-specific with regard to their mycorrhizal fungus.

FRUCTIFICATION.

Plate II shows a fructification of *Corticium solani* on the leaf sheath and basal leaf blade of a plant of *O. purpurella* found on Scotstoun Moor. The record refers to one plant only; an intensive search for further specimens proved unsuccessful. The fructification was immature and therefore basidiospore measurements could not be made, but the hymenium and young basidia were similar to those of *C. solani* on potato at a comparable stage in development (Plate III). An orchid endophyte belonging to the genus *Rhizoctonia* which develops its perfect stage under natural conditions has not heretofore been recorded but with the recognition of *C. solani* as a symbiont of *O. purpurella* this position is revised.

DISCUSSION.

Orchid endophytes fall into two groups, one containing forms referred to the genus *Rhizoctonia* and the other consisting of fungi with clamp-bearing hyphae. In the latter group some species have been identified and are recognisable in their natural surroundings outwith the orchid. The fungi in the *Rhizoctonia* group on the other hand are known only within the tissues of the root and as isolates in culture. The acceptance of *Corticium*

solani as an orchid endophyte alters this position. *C. solani* is an important plant pathogen attacking a variety of hosts and a considerable amount of information, morphological, ecological and physiological has been published about this species. An attempt will therefore be made to evaluate the status of the *Rhizoctonia* spp. known only as endophytes on the basis of the data accumulated for the pathogen. It has been said of *C. solani* that "In culture the races differ in colour; zonation of colony; type of growth, that is, suppressed or aerial mycelium; number, size and position of sclerotia; aggregation of sclerotia; diameter of hyphae; and rate of growth" (Kernkamp *et al.*, 1952). This statement could describe the variation encountered in *Rhizoctonia* endophytes and these variations have been used to define species in this group. But are they indeed true species or might some of them prove to be strains of *C. solani*? *Rhizoctonia neottiae* Wolff—isolated from the roots of *Neottia nidus-avis* L. and of *Aplectrum hyemale* Torr., unaccepted as a symbiont by the seed of the former orchid (Burgeff, 1936) but accepted by the latter (Curtis, 1939), has the colour, sclerotial structure, hyphal and sclerotial cell measurements of isolates of *C. solani* from potato. *R. borealis* Curtis, isolated from *Goodyera repens* var. *ophiodes* and *Spiranthes gracilis*, has brown mycelium and sclerotia and although the sclerotial cells are shorter and wider than typical strains of *R. solani* the difference in measurements is not excessive. On the other hand the majority of *Rhizoctonia* endophytes are white or cream coloured, have finer hyphae with binucleate cells and seldom develop discrete sclerotia, but sclerotial development in *R. solani* can be suppressed under varied cultural conditions (Kernkamp, 1952) while all the other features are to be found in strains of the pathogen (e.g. isolates from cauliflower and wheat). Though proof must await experimentation the suggestion is put forward that among the varied strains of *C. solani* potential, if not actual, symbionts of a number of orchids may be discovered.

It has generally been assumed that the *Rhizoctonia* endophytes exist outwith their hosts as soil saprophytes or facultative parasites but little proof is available of their distribution in the soil. *R. goodyerae-repentis* has been shown to occur in the pine-needle litter in Aberdeenshire where the orchid is widely distributed (Downie, 1943) and also in Hampshire and Somerset

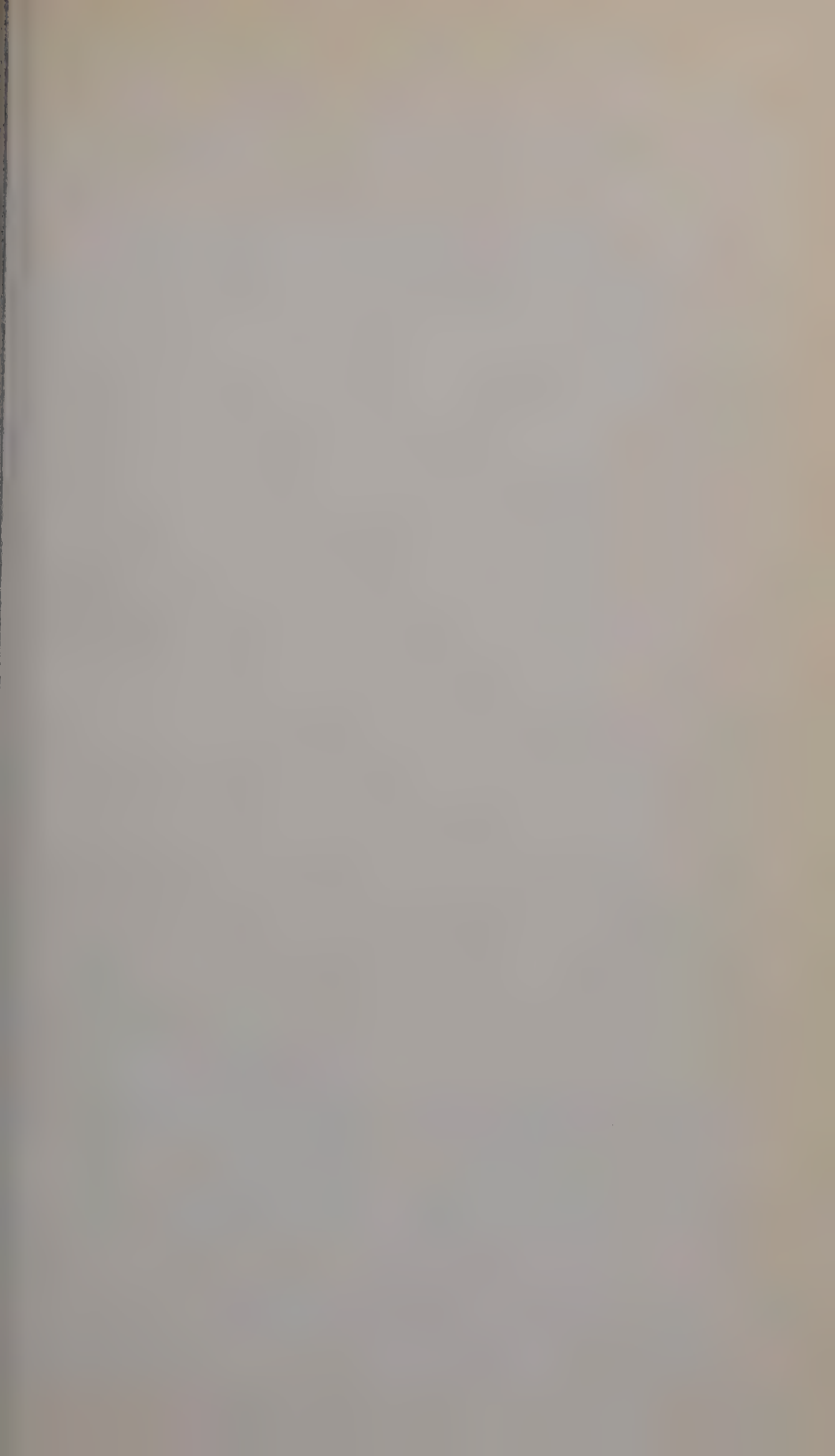


PLATE III



1



2



3

Fructification of *C. solani* on *O. purpurella*.

(1) Hymenium and basidia $\times 118$, (2) Immature basidia $\times 336$,
(3) Developing basidiospore and immature basidia $\times 336$.

where the orchid does not occur (Downie, unpublished data). The widespread occurrence of *Corticium solani* as a soil saprophyte has been frequently demonstrated (Blair, 1943; Chesters, 1948; Garrett, 1951). It has the ability to develop extensive sparse colonies, an ability shared by other *Rhizoctonia* endophytes. The fact that *C. solani* is an orchid endophyte therefore lends support to the original assumption.

Deterrent factors in the identification of *Rhizoctonia* endophytes have been lack of recognition of the perfect stage and the failure to induce fruiting in culture. Two exceptions have been recorded where *Rhizoctonia* endophytes gave rise to fruiting bodies in culture, i.e. *Corticium catonii* Burgeff, and *C. masculi* Sprau. These were chance occurrences, however, and have not been repeated in culture for either species. Some doubt must be expressed as to the authenticity of *C. masculi* as the fructification of an orchid endophyte. From the description and diagrams this fungus seems to be identical to the air-borne species *Trechispora brinkmanni* (Bres.) Rogers & Jackson. The latter appeared as a contaminant in one of my own *Rhizoctonia* cultures and because of its similarity to *C. masculi* was at first assumed to be a chance fructification of the endophyte. Germination tests with seed of the appropriate orchid and of *Orchis mascula* L. failed to establish symbiosis and therefore acceptance of the fructification as that of the endophyte was in abeyance. Dr. C. J. Hickman very kindly drew my attention to the similarity of my isolate with *T. brinkmanni* and sent a culture of the latter to me. On comparison it was found that the isolate previously assigned to *C. masculi* was identical with *T. brinkmanni*. In his treatise on *Trechispora* and *Galzinia*, Rogers (1944) places *C. masculi* in the complex of fungi he denotes as *T. brinkmanni* but quotes it as a nomen nudum. The description of *C. masculi* by Sprau was based on material in culture and no specimen exists for comparison. Sub-cultures of a fungus listed in the collection of the Centraalbureau voor Schimmelcultures, Baarn, Holland, as *C. masculi* Sprau failed to show any of the described diagnostic features—the hyphae were without clamps and neither oidial cells nor basidia developed when the fungus was cultured on a variety of laboratory media. *C. masculi* may have been a distinct species but the fact that a very similar fungus occurs as a not infrequent culture contaminant as evidenced by Dr. Hickman,

Prof. Ingold and myself seems to warrant the tentative rejection of this fungus as the fruiting form of an orchid endophyte.

Attempts to secure the fructifications of the forms of *R. solani* isolated from *O. purpurella* have not so far been made, but the fungus is known to fruit freely on the stems of the potato and a similar fructification has been observed on *Orchis purpurella*. An orchid endophyte of the *Rhizoctonia* type which fruits under natural conditions can therefore be recorded. Considering the wide distribution of the fungus and the variety of hosts it attacks the paucity of fruit bodies developed by this species is an interesting feature which may be significant in assessing the lack of fructifications among other *Rhizoctonia* endophytes.

SUMMARY.

1. *Orchis purpurella* T. & T. A. Steph. is non-specific with regard to its associated symbiotic fungus.
2. Proof is submitted that *Corticium solani* (Prill. & Delacr.) Bourd. & Galz; stat. mycel. *Rhizoctonia solani* Kühn (Syn. *Pellicularia filamentosa* (Pat.) Rogers) is a frequent endophyte in the roots of *O. purpurella* and is an accepted symbiont at seed germination.
3. Suggestions are put forward that strains of this fungus may be actual and potential symbionts of other orchids.
4. The distribution of *C. solani* as a widespread soil saprophyte and facultative parasite is thought to reflect on the soil ecology of other orchid endophytes.
5. An orchid endophyte of the *Rhizoctonia* type which develops its fruit body under natural conditions is now recorded.

ACKNOWLEDGMENTS.

I wish to express my indebtedness to Mr. P. J. Faulks of this department for the statistical analysis of hyphal measurements; to Dr. M. Henderson of the Macaulay Institute for Soil Research for the corroboration of the nuclear condition of hyphal cells by fluorescent microscopy and to the senior technicians, Mr. I. Moir and Miss F. Greig for the photographic records.

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EXPLORATION OF THE SCOTTISH FLORA.

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A convenient starting point to this essay is the year 1684. Only a very little was known of the flora of Scotland before then, and records of the occurrence of Scottish plants were very few and isolated. James Cargill for instance, a doctor of Aberdeen and a former pupil at Basle of Casper Bauhin, had sent to Bauhin in 1603 certain specimens which Bauhin recorded in his *Prodromus* of 1620—"In betulis Scotiae natans". The specimens in question were those of the Chickweed Wintergreen, *Trientalis europaea*, and *Trientalis* was thus the first recorded Scottish plant. Parkinson in his *Theatrum Botanicum* of 1640 had recorded *Pyrola rotundifolia* as well as the Scots Pine. The great naturalist John Ray had paid his first visit to Scotland in 1661 and had not been impressed. "They are not very cleanly in their houses, and but sluttish in dressing their meat . . . they have neither good bread, cheese or drink . . . their butter is very indifferent, and one would wonder how they could contrive to make it so bad . . . they have rarely any bellows, or warming pans . . . the people seem to be very lazy, and may be frequently observed to plough in their cloaks . . . they layout most they are worth in cloaths and a fellow that hath scarce 10 groats besides to help himself with, you shall see come out of his smoky cottage clad like a gentleman". Still, Ray visited the Bass Rock where he saw Gannets, Guillemots and Black Guillemots, Kittiwakes, and Shags, as well as *Beta maritima*, *Silene maritima*, *Cochlearia officinalis* and *Lavatera arborea*; came to Leith and to Edinburgh—saw the Castle, Heriot's Hospital and the College; went to Stirling by Linlithgow and on to Glasgow—"the second City in Scotland, fair, large and well built, cross-wise, somewhat like unto Oxford"; south to Hamilton and on to Douglas in Lanarkshire where on Lowther Hill he saw *Lycopodium alpinum*; then past the Lead Hills to Dumfries and south to Carlisle. In 1670, Thomas Willisel had added to the British Flora *Viscaria vulgaris* from the Cliffs of Samson's Ribs and the find is recorded in Ray's Catalogue of Plants published in that year. And in 1671, Ray had paid his

second visit to Scotland, finding *Sisymbrium irio* on the walls of Berwick and two miles from Berwick a plant new to science, *Tofieldia pusilla*, as well as *Mertensia maritima* which Willisel had discovered the year before.

This, then, was the state of affairs in 1684, the year in which Sir Robert Sibbald, who founded the Royal Botanic Garden, Edinburgh, published a natural history of Scotland under the title of *Scotia Illustrata sive Prodrromus Historiae Naturalis*, etc. The first part deals with geographical and archaeological details whilst the second part enumerates nearly 500 plants as well as colour forms and varieties. Some of the plants are rather difficult to identify, whilst many of the species are not really natives in Scotland at all. Only two species are recorded for the first time as British, *Sibbaldia procumbens*, named after Sibbald of course, and the umbelliferous plant *Ligusticum scoticum*. There are many references to plants in the neighbourhood of Edinburgh and probably the most interesting of these are *Viscaria vulgaris*, discovered by Willisel in 1670, and *Asplenium septentrionale*—both on Salisbury Crags, where they still grow.

In the *published* accounts of the next ninety years we find nothing but isolated records of Scottish plants, such as Martin Martin's mention in his *Description of the Western Islands of Scotland* (1703) of *Dryas* in a locality 1,000 yards from Ben Suardal near Broadford in Skye, probably the first record for *Dryas* in Britain; *Carum verticillatum*, near Ayr, in Martyn's *Tournefort* of 1732; Dr. John Walker's finding of *Oxytropis uralensis* near Loch Leven in 1761; and the discovery in Skye of the Pipewort, *Eriocaulon septangulare*, by Sir John Macpherson in 1764, and again in 1768 by James Robertson. Hudson's *Flora Anglica*, first published in 1762 and an excellent compilation of existing knowledge of the British Flora, contains only a few Scottish records.

For the next considerable advance in the *published* record we have to wait until 1778, when the *Flora Scotica* of the Rev. John Lightfoot was published, although the title page is dated 1777. Lightfoot's journey through Scotland was undertaken in 1772 at the invitation of the celebrated zoologist and antiquary, Thomas Pennant, who travelled with him.

Though the itinerary is not given in detail, much of it is not difficult to piece together. They journeyed "either by land or

sea from the South of Annandale to the borders of Sutherland". On the way north to Sutherland, they visited the Isle of Arran where *Carex pauciflora* was added to the British Flora, and the islands of Bute, Jura, Colonsay, Iona, Islay, Mull and Rhum. On the mountains of this last-named island, and on Barkeval especially, they found *Tofieldia*, *Saxifraga oppositifolia*, *Silene acaulis*, *Cherleria sedoides*, *Thalictrum alpinum*, *Cardaminopsis petraea* and *Salix herbacea*. In Skye, the recently-discovered *Eriocaulon* was seen, as well as *Pinguicula lusitanica*, *Polygonum viviparum*, *Utricularia minor*, *Dryas*, *Arctostaphylos alpina*, *Hieracium alpinum*, *Coeloglossum viride*, *Botrychium lunaria*, *Cryptogramme crispa* and *Isoetes*. From the islands they came to Loch Maree where they gathered *Hymenophyllum* and *Circaea alpina*; on the way to Dundonnell they added two orchids to the British Flora, *Goodyera* and *Corallorhiza*, neither of which has been seen in this locality since, as well as *Pyrola secunda* and *P. minor*. They explored Little Loch Broom and the mountains at the head of the loch whereon they gathered *Chamaepericlymenum suecicum* and *Vaccinium uliginosum*. Thence, by way of Creg-a-chnocaen—the boundary of Coygach and Assynt—where they gathered *Dryas*, *Polystichum lonchitis* and *Asplenium viride* and, in the lochs, *Sparganium*—on to Tongue in Sutherland. On the return journey they did considerable exploration in Perthshire and probably visited Blair Atholl and Forfar on their way to Edinburgh and Kelso.

About 1,250 species, phanerogams and cryptogams, are listed in the *Flora*, and well over fifty of these are alpine flowering plants. For the first time the richness of the flora of the Breadalbane mountains was made known, and Craig Caillich, Meall Ghaordie, Meall-nan-Tarmachan and Bein Heasgarnich are familiar names on the pages of the *Flora*. This was due in the main to a Perthshire botanist, the Rev. John Stuart of Killin, who, in 1772, not being ordained to a charge, accompanied Lightfoot on his journeys. He was then 29. After his journey with Lightfoot he became Minister of Luss where he died in 1823. His father translated the New Testament into Gaelic and he translated the Old Testament. Published in 1767 the two became the Standard Gaelic Bible. About a year before he died John Stuart received £1,000 from the Government. How industrious and helpful Stuart was can be gathered from the fact that of the

119 plants which Lightfoot recorded for Perthshire, 47 are directly credited to Stuart including *Oxytropis uralensis*, *Hieracium alpinum*, *Gnaphalium supinum*, *Saxifraga nivalis*, *Dryas*, *Poa alpina*, *Chamaepericlymenum* and *Juncus triglumis* and *J. biglumis*. Strangely enough, for Stuart had lived in Killin and was familiar with the flora of Ben Lawers, not one plant from this mountain is recorded by Lightfoot.

Lightfoot, in the preface to the *Flora*, acknowledges his indebtedness to several scientists, among them Professor John Hope, Professor of Botany in Edinburgh "who not only favoured me with the sight of his copious Herbarium, but permitted me the use of his notes and observations, the result of a long enquiry". From an examination of certain notebooks of Hope which are in the Library of the Royal Botanic Garden, Edinburgh, it is quite clear that he and his students had collected widely in Scotland, not only on the mainland but in Arran, Skye, Mull, Orkney and Shetland as well, and no doubt Hope influenced Lightfoot in the planning of his Scottish Itinerary. It is also clear that Hope and his colleagues had collected quite a number of Scottish plants some years before they had been found by others and published as new records for the Scottish or British Flora. For instance in 1768 *Erigeron borealis* was in Hope's Herbarium, having been collected by Stuart on Ben Lawers; yet the first finding of this plant is usually attributed to James Dickson who gathered it on Lawers in 1789. Dickson likewise is claimed to be the discoverer of *Veronica alpina* on Ben Nevis in 1789, yet Hope records it as having been collected by Dr. de la Roche and Fabricius, Edinburgh Medical Students, in 1767 on the same mountain. George Don is regarded as having added *Eriophorum alpinum* to the British Flora when he found it in Restennet Moss, Forfarshire, in 1791, yet a specimen appears to have been in Hope's Herbarium in 1768. James Brebner in 1884 has the credit for discovering *Schoenus ferrugineus* when he found it growing beside Loch Tummel, but apparently there were specimens in Hope's Herbarium in 1768 gathered in Skye where it has not been found since. There are many other similar examples.

Obviously Lightfoot's work made a tremendous advance in the knowledge of the plants of Scotland. Even so, it met with severe criticism, and Pennant withdrew the books and "imprisoned them for a few years in a darksome cell of a London

warehouse". There they remained until 1792 when Pennant reissued the *Flora* under the somewhat misleading title of "Second Edition". Round about this date more records of Scottish plants were gradually accumulating and the treasures of Ben Lawers were revealed in print for the first time. James Dickson, born at Traquhair, Peebles, in 1738, and a Covent Garden Nurseryman, paid two visits to Scotland and between 1793 and 1802 issued a set of nineteen fasciculi of plants. In 1789 he gathered on Lawers *Veronica fruticans* and *Draba rupestris*—both new records for our flora—as well as *Erigeron borealis*, in the discovery of which, as we have seen, he had been forestalled by Stuart. Three years later (1792) and on the same mountain, Dickson discovered *Saxifraga cernua* and *Gentiana nivalis*.

Lawers was also familiar ground to another Nurseryman, this time of Forfar, the illustrious George Don who had for some years been eagerly exploring the Highlands of Scotland. This Don himself tells us in the preface to his *Herbarium Britannicum* (1804) a work dedicated to Sir Joseph Banks, then President of the Royal Society; four fasciculi, each of twenty-five plants and containing a due proportion of rare alpine, were to be issued yearly. He says:

"Since he first began his botanical excursions into the Highlands of Scotland, in the year 1779, he is confident (and he hopes he may mention it without the imputation of vanity) that he has traversed more of the Caledonian alps than any other botanist has ever done. He has repeatedly ranged over the great mountains of Angus which surround the great district of Clova, where no one on a similar pursuit has ever preceded him. He has also searched the vast range of mountains which stretch about sixty miles through the district of Knoydart, in Inverness-shire, a region which had never before, nor has since, been examined with a botanical eye. He is the only botanist, too, who has explored the lofty mountains of Cairngorm and the great hills of the neighbourhood."

During his frequent visits to Ben Lawers he collected that rare Sandwort, *Arenaria rubella* (now *Minuartia rubella*), the beautiful Forget-me-not, *Myosotis alpestris*, and a sedge, *Carex atrofusca* (all new to the British Flora), the rare mountain fern, *Woodsia hyperborea* (now *W. alpina*) and the three rushes, *Juncus biglumis*, *J. bulbosus* and *J. castaneus*. For the first time

in Scotland, he located *Bartsia alpina* and also saw the Alpine Sandwort, *Sagina linnaei*, on Meall Ghaordie. *Carex vaginata* was his outstanding find on Cairngorm, and *Luzula arcuata* on the great bulk of Ben Macdhui. Time and time again Don explored Clova and was the first to make known to botanists this beautiful district of Angus. Here he discovered *Carex rari-flora* and *Hieracium calenduliflorum*, both new to science, *Hieracium lingulatum* and *Oxytropis campestris*, and on Little Culrannoch, *Viscaria alpina*, all new additions to the British flora. On distant Ben Nevis, he gathered the alpine form of *Sagina maritima* and the rare grass *Poa flexuosa*; on Ben Lomond in 1789 he saw *Carex saxatilis* four years before Dickson found it on Lawers in 1793, and *Cerastium alpinum*; a form of the latter from Ben Chonzie he misidentified as *C. latifolium*; Ben Vorlich yielded *Saxifraga oppositifolia* and Schiehallion *Carex vesicaria* and *Thalictrum alpinum*. His many ascents of Lochnagar revealed the riches of the alpine flora of this grand mountain. Here he found the Alpine Foxtail, *Alopecurus alpinus*—a species new to science—as well as such rarities as *Cochlearia alpina*, *Hieracium calenduliflorum*, *H. globosum*, *Saxifraga rivularis*, *Lactuca alpina* (now *Cicerbita alpina*) and the grasses, *Deschampsia alpina* and *Poa* × *jemtlandica* (*alpina* × *flexuosa*).

Don's most important publication was *An account of the Native Plants in the County of Forfar, and the Animals to be Found There*. This formed an appendix to the *General View of the County of Angus or Forfar*, by the Minister of Dunnichen, the Rev. James Headwick. The work appeared in 1812, and Don contributed forty-nine pages in which he enumerates 90 species of flowering plants, 100 mosses, and 120 lichens from Clova. Altogether nearly 300 "larger plants" are listed, and most of these, he says, could be seen growing in his garden at Forfar.

Of this Forfar garden there is a most interesting account in *The Scots Magazine* for June 1809. The writer is Don's friend, Dr. Patrick Neill of Canonmills, Edinburgh. "The existence of a flower garden and flower nurseries at Forfar, which for number, diversity, and rarity of the hardy plants cultivated in it are perhaps scarcely to be surpassed in Britain, is a fact not generally known. The garden is situated on a bank which slopes down to the lake of Forfar, not far from the town; and it fortunately includes a great variety of soils, from dry to peat bog To

give some idea of the extent of the collection, I shall mention the number of species of several genera which are at present growing in the garden. Of the genus *Veronica* there are 55 species, of *Salvia* 50 species, *Campanula* 44, *Allium* 40, *Saxifraga* 46—some of the rarest ones, as *S. caesia*, *S. petraea*, *S. rivularis*, etc.; *Dianthus* about 20 species, *Cucubalus* 13—being the whole ever cultivated in Britain; *Silene* nearly 50, . . . the genera *Ononis*, *Lathyrus*, *Vicia* almost complete, *Astragalus* 40 species, *Trifolium*, no fewer than 69, *Hieracium* 44. It were needless to enumerate more. The botanist will form a due estimate of this collection on being told that he may see here upwards of 60 species of *Carex* flourishing in great perfection. The agriculturist may here find the whole of the hardy Gramina, carefully distinguished and arranged, amounting to over 100 kinds. This season Mr. Don has introduced several hundred species of hardy plants, most of which we are told have never before been cultivated in Scotland."

No doubt Don's garden was in no wise different from other botanic gardens. No doubt his labels became misplaced and one species invaded the territory of another, with the result than Don recorded some alien species as British. No doubt some of Don's localities are so vague that plants have not since been found in the localities he gave to them. Allow all this—and one still must wonder at the amazing industry and constitution which enabled him to tread so far afield, and allowed him to record so many new plants to his country's flora.

Don and Hope were the pioneer explorers in Scotland. Others followed—Thomas Drummond, who took over Don's Forfar Garden, later became Curator of the Belfast Botanic Garden and accompanied Franklin on his second Arctic Expedition, issued two fasciculi of Scottish Mosses, recorded *Salix lanata* from Clova and discovered *Lathyrus niger* in the Den of Airlie, West of Forfar; Robert Brown, the Perth Nurseryman, who found *Phyllodoce caerulea* at Aviemore in 1812; William Borrer, friend of Sir James Edward Smith and Sir William Jackson Hooker, who added *Nuphar pumila* and other plants to our Flora; Arthur Bruce, Secretary of the Natural History Society of Edinburgh, who in 1792 recorded *Polygonatum verticillatum* near to Dunkeld; Thomas Hopkirk of Paisley, author of *Flora Glottiana* (1813), an enumeration of plants mainly obtained from the banks of the Clyde and the neighbourhood of Glasgow, some 662 species

in all, of which about 40 are additions to the Scottish Flora, but most of them aliens and casuals; Dr. Walker Arnott of Glasgow who tried to discredit so much of Don's good work; Dr. Alexander Murray of Aberdeen, author of the *Northern Flora*, a description of the wild plants of the North and East of Scotland; the two Mackays—John of Leith Walk Nurseries and Principal Gardener of the Royal Botanic Garden from 1800 to 1802, who in 1794 discovered *Eleocharis multicaulis* and, very doubtfully, *Pinguicula alpina* in Skye, and James Townsend Mackay of Kirkcaldy and later Curator of Trinity College Gardens, Dublin who did so much for the Irish Flora; James Brodie of Brodie who in 1793 found *Moneses grandiflora* the same year in which this plant was sent to the Linnean Society by Mr. James Hoy, a Gardener at Gordon Castle; Professor Beattie of Aberdeen, the discoverer of *Linnaea borealis* in the pinewoods of Mearns in 1795. The findings of all these—and of others—are partly recorded in the 36 volumes of *English Botany* by Sir James G. Smith who, in 1787, had gathered *Luzula spicata* on Ben Lomond, but more fully in the *Flora Scotica* of Sir William Hooker in 1821. In this work, dedicated to the Duke of Montrose, about 90 species are added to the Scottish Flora and to George Don, either wholly or in part, nearly 50 records are due. The great interest of the Scottish mountain flora at last was revealed to the botanical world.

Thus until the early eighteen hundreds, Scottish botany—and of course English, Welsh and Irish Botany as well—was chiefly concerned with the collecting and identification of the native flora. The plants were there, awaiting discovery, and the Hopes and the Dons and all the others were pioneers who could not fail to make important and often exciting new additions to the number of plants already known. In 1830 Sir William Hooker published the first edition of the *British Flora*, and eight editions were to appear in the course of the next thirty years. Previous to the *British Flora*, the written records, with one or two important exceptions, had aimed chiefly at indicating the locality where any particular plant was to be found. But the *British Flora* was meant to do more than this, for in the preface Hooker very significantly avows himself "rather anxious to indicate the range of the species than the precise spot where any one is found". Thus British botanists were becoming alive to the interests of the distributional problems of their native plants.

In this Hooker was not the pioneer. The honour falls to Nathaniel Winch, who, in 1819, read at a Meeting of the Literary and Philosophical Society in Newcastle upon Tyne a very remarkable paper entitled "An Essay on the Geographical Distribution of Plants through the Counties of Northumberland, Cumberland and Durham".

After briefly discussing the topography of the country, the indigenoussness or otherwise of some of the trees such as the Oak, Elm, Beech, Ash, Aspen and Pine, of the exotics which succeed in woods and plantations, and the past and present distribution of agricultural land, Winch divides the plants of the three Northern Counties into certain groups: those plants which have reached their Northern Limits in this part of the Kingdom; those plants which have reached their Southern limits; those which are found on the Sea Coasts, and again on the Mountains; rare species, natives of Switzerland; rare species, natives of Lapland; rare species, natives of both these countries; rare species, natives of neither of these countries; etc.

This analysis of a particular portion of the British flora from a phyto-geographical point of view is something quite new. Likewise is William MacGillivray's ecological and altitudinal study of the plants in an area in Aberdeenshire—*Remarks on the Phanerogamic Vegetation of the River Dee*, published in 1832. MacGillivray describes the alpine vegetation and traces it downwards from the mountain tops as it mingles with the vegetation of the valleys. Gradually descending, he lists the plants which creep down the mountain and those of lower situations which struggle upwards, noticing their habitat and any changes in their vegetative and reproductive condition, until he reaches the heaths and moorlands and finally the valleys.

Both Winch and MacGillivray expressed the hope that their fragmentary studies would stimulate others to prepare a complete picture of the geographical distribution of British Plants. In this they were not to be disappointed. Shortly after the publication of MacGillivray's short paper, in the same year of 1832 in fact, there was printed for private distribution a small volume entitled *Outlines of the Geographical Distribution of British Plants*. The author was Hewett Cottrell Watson.

Watson was born at Firbeck in Yorkshire in 1804. At the age of 22 he was placed in independent circumstances, and not

being able to follow a military career owing to a knee injury sustained when he was a boy, came to Edinburgh to study medicine. But on his health failing just before he was due to sit his Final Examination, and, in any case, not wanting to practice medicine, he left Edinburgh and after a short period of travel, finally settled in Thames Ditton in Surrey in 1835, to devote himself to the study of botany, the elements of which he had learned from Bishop Stanley during his childhood in Yorkshire.

As a student in Edinburgh, Watson had taken great interest in the botanical lectures of Professor Graham whom he accompanied on an excursion to Sutherland. Graham introduced him to Sir William Hooker and he was a frequent companion of Hooker and his students on many of their Highland excursions. His writings on the geographical distribution of the British flora covered a period of over 40 years and the *Outlines* is his first botanical publication.

After the *Outlines* for nearly a quarter of a century this industrious man was compiling what was to prove his magnum opus—*Cybele Britanica*, or British Plants and their Geographical Relations—a work of four volumes, the first of which appeared in 1847 and the last in 1859. 'Cybele' was the mythological name of a Goddess who was supposed to preside over the productions of the earth, and Watson proposed this term for an account of the geography of the plants of any particular country as a parallel to the term 'Flora' which had so long been used for a systematic description of the orders, genera and species of any given region. The *Cybele* is a systematic treatise on the geographical distribution of the plants in the counties of Britain and embodies the author's plans for registering the details of plant distribution. These, of course, are so familiar to all botanists that it would be a work of supererogation to explain them here.

In 1860 Watson published a Supplement to the *Cybele* in which he traced the horizontal range of British species through the 38 subprovinces into which he had divided Britain. A mass of additional material which he harvested in the years following the publication of his last volume of the *Cybele*, formed the text of the three volumes of the *Compendium of the Cybele* (1868-70) wherein he worked out the distribution of the species beyond the borders of Great Britain. Lastly, in the two volumes of

Topographical Botany (1874-75) with a second Edition in 1883, the horizontal distribution of the species is traced through the 112 vice-counties into which he had further divided the country. This work was compiled from a great mass of material for which many botanists were responsible. In Scotland, there was William Gardiner, the umbrella-maker of Dundee who in 1848 published the *Flora of Forfarshire* wherein is to be found a most excellent description of the mountainous part of the county known as the Clova district. There was the author of the *Scottish Cryptogamic Flora* (1823-28) and the *Flora Edinensis* (1824), Robert Kaye Greville, who was joint discoverer of two rare alpines, *Carex alpina* (now known to be the same as *C. norvegica*) and *Astragalus alpinus*. There were the Professors of Botany of the Scottish Universities: George Dickie of Aberdeen, author of the *Botanist's Guide to the Counties of Aberdeen, Banff and Kincardine* (1860); Robert Graham who occupied first the chair of botany in Glasgow before coming to Edinburgh, who added *Ononis reclinata* to the British Flora from the Mull of Galloway in 1835 (although there is a fragment in the Edinburgh Herbarium dated 1833 and carrying the name of Dr. Balfour) and who recorded *Thlaspi alpestre* (Caenlochan 1832), *Saxifraga caespitosa*, and with Greville and Brand discovered *Astragalus alpinus* in Clova in 1831; and John Hutton Balfour of Edinburgh who yearly made excursions into the mountains of Scotland with his students. Balfour was in the habit of writing up short accounts of these excursions and some of them are quite remarkable not only for the number of alpine plants which were recorded, but for the idea they give of the temperament and attitude of mind to the job in hand of these outstanding botanists. For instance, in the Edinburgh New Philosophical Journal for July 1848, Balfour prefaces his account of a three-weeks excursion in 1847, to the richest alpine districts in Britain—the mountains of Braemar, Glen Isla, Clova and Ben Lawers—with these remarks:—

“Excursions may be truly said to be the *life* of the botanist. They enable him to study the science practically, by the examination of plants in their living state, and in their native localities; they impress upon his mind the structural and physiological lessons he has received; they exhibit to him the geographical range of species, both as regards latitude and altitude; and with the pursuit of scientific knowledge, they combine that healthful

and spirit-stirring recreation which tends materially to aid mental efforts. The companionship too of those who are prosecuting with zeal and enthusiasm the same path of science, is not the least delightful feature of such excursions. The various phases of character exhibited, the pleasing incidents that diversify the walk, the jokes passed, and even the very mishaps or annoyances that occurred—all become objects of interest, and unite the members of the party by ties of no ordinary kind”.

The most outstanding of these “mishaps or annoyances” occurred in the same year of 1847, when Balfour and his party, accused of trespassing, had a skirmish with the Duke of Atholl and his retainers. A lawsuit followed and the notorious “Battle o’ Glen Tilt” was celebrated in verse and pictures.

Hutton Balfour was also closely associated with the Scottish Alpine Botanical Club; in fact, he was one of the original members when the club was formed at Bridge of Lochy Hotel on the 10th August 1870. Yearly the Alpine Club visited the Scottish Highlands, with an occasional diversion elsewhere, to Teesdale, or Ireland, or even Norway. Among many notable discoveries may be mentioned Bayley Balfour’s discovery of *Gentiana nivalis* on Cham-a-creag in October 1872; John Sadler’s finding of *Salix* $\times$ *sadleri* (*S. herbacea* $\times$ *lanata*) in Corrie Ceann-mor, Aberdeenshire, in 1874; Boyd’s new station at Lochaber for *Saxifraga caespitosa* in 1886, and—perhaps—the remarkable *Sagina boydii*, which has not been seen since, during the Braemar excursion of 1883; Dr. Paul’s gathering of *Carex atrofusca* on Ben Lawers in 1892, thus confirming the original discovery of the plant on the same mountain by Don eighty-two years before; Paul’s finding of *Saxifraga caespitosa* on Ben Avon, the mountain which divides Banffshire from Aberdeenshire, in 1899. This rare British alpine had been gathered on Ben Avon in 1831 and 1832, but from then until 1899 it was not found. Accounts of many of the expeditions of the Scottish Alpine Botanical Club are to be found in the *Transactions of the Botanical Society of Edinburgh*.

On the 28th February, 1867, fourteen naturalists met in a room of King James the Sixth’s Golf Club, Perth, and formed the Perthshire Society of Natural Science, with one of their number, Francis Buchanan White, as the first President. This Society was destined to make important contributions to the natural history of Perthshire, especially to the distribution of the Perth-

shire alpine plants in relation to the geological formation of the country. An offset of the Society was the Perthshire Mountain Club which held at least one excursion to the higher mountains of the county each year. White, a lover of both mountains and mountain plants, chose as the emblem of the Club that characteristic alpine, *Salix herbacea*, the smallest of British willows. From 1867 until his death in 1894, White communicated a hundred or so papers to the Society, most of them published in the *Proceedings and Transactions*. Moreover, under his editorship *The Scottish Naturalist* became the official Journal of the Society in 1870, and remained so for 22 years when it was merged with the *Annals of Scottish Natural History* in which so soon after White's death, Professor Trail was to commence the publication of the *Topographical Botany of Scotland*. And to James Trail fell the task of editing White's crowning achievement, *The Flora of Perthshire*, published posthumously in 1898, four years after White died.

The Perthshire Society of Natural Science was but one of many such Societies formed in Scotland during these years. The Berwickshire Naturalists' Club (1831), The Natural History Society of Glasgow (1851)—now The Andersonian Naturalists of Glasgow, The Dumfries and Galloway Natural History and Antiquarian Society (1862), The Edinburgh Natural History Society (1869)—these, and others, played an important role in increasing our knowledge of the flora of Scotland.

During these years there were those in Scotland who would have awarded the palm for the best botanical knowledge of Scotland to a Yorkshireman, James Backhouse, Junior. For many years Backhouse botanised with his father and from 1845 father and son often came to Scotland, chiefly hunting *Hieracium*, for whose monograph of the British species the son will always be best known. At this time (1856) little attention had been given to this very critical genus and the task of turning a mass of almost unknown material into systematic order could have been no easy one. It is sufficient to say that Backhouse described eleven new species, eight of which are still cited in the *Check-List of British Vascular Plants* for 1946, and all eleven maintained in Pugsley's *Prodromus of British Hieracia* in 1948.

Watson's topographical work had, of course, to be continued after his death in 1881. Many records were of very doubtful and

imperfect nature and for some districts almost none was available. Thus there were many gaps to be filled and much checkwork to be done. Moreover, there were critical genera such as *Hieracium*, *Rubus* and *Rosa* which were requiring close and detailed study. None worked more industriously in the performance of these various tasks than Arthur Bennett. By trade a builder and house decorator, Bennett devoted much of his spare time over a period of more than fifty years to the elucidation of critical genera and became a recognised authority on the genus *Potamogeton*, so much so that he was entrusted by the authorities of Kew and the British Museum with the naming of pondweeds from all parts of the world. And it was he who completed Fryer's *Potamogetons of the British Isles*. Always, one of his great interests was the topographical distribution of plants. Realising the need for systematic work on the flora of some of the northern counties, he began publication in 1886 in the *Scottish Naturalist* of *Additional Records of Scottish Plants*, records which continued yearly until 1891, and after this date were published in the *Annals of Scottish Natural History* until 1905.

There is no doubt that Bennett's interest in Scottish plants was part and parcel of his love for the floras of Scandinavia, Iceland and the Faroes, and from a paper in volume II of the *Scottish Naturalist* in 1885, it is very obvious that he was fully alive to the floristic affinities of these areas. Enumerating the plants of Iceland and of the Faroes which do not occur in Britain, he mentions *Arabis alpina* and comments thus:—"Looking at the European distribution of this species, it seems strange that it is not British (Sicily, Greece and Tartary being the only other stations in which it does not occur)". Only two years afterwards, in 1887, H. C. Hart discovered the plant on the wet rocky ledges of the Cuillin Hills of Skye. Of *Carex capitata* and *C. microglochin* he says:—"Might well be passed over as *pauciflora*". *C. microglochin* was added to the Scottish flora in 1923 when it was found in Glen Lyon by Lady Davy and Miss Bacon. *C. capitata* is now also known to be a Scottish plant for it was found by Professor Heslop Harrison in South Uist in 1942. Two other sedges listed by Bennett, *C. chordorrhiza* and *C. pedata* (now to be called *C. glacialis*) have been added to our flora since 1885, the former at Alltnaharra in West Sutherland in 1897 and the latter on the Island of Rhum in 1943.

It is a strange thing that during these years when Arthur Bennett was examining so many Scottish Plants and publishing so many records, he did not once visit Scotland. Be that as it may, in 1905 he was able to publish the first *Supplement to Topographical Botany*, thus bringing Watson's work up to date and incidentally recording the names of those botanists who had been active in extending our knowledge of the distribution of Scottish plants. The *Supplement*, of course, incorporates all Bennett's work on Scottish plants as well as Professor Trail's communications to the *Annals of Scottish Natural History* on the *Topographical Botany of Scotland*, papers which commenced in 1898 and continued for four years after the publication of the *Supplement*. With the appearance in the *Journal of Botany* in 1929 of the *Second Supplement*, compiled by Arthur Bennett, C. E. Salmon and J. R. Matthews, and listing records up to the end of 1925, the firm groundwork of British Topographical Botany was established.

Thus for a considerable number of years botanists had been showing great activity in the critical examination of species and of their frequently numerous forms, and in comparing these with their continental representatives. Apart from Bennett I need but mention Hanbury's work on *Hieracium*, Townsend's work on *Euphrasia*, the Rev. E. S. Marshall's work on both these genera, and Wolley-Dod's revision of the British roses.

Though he never studied intensively, or became an authority on, any particular group of so-called "critical" plants, George Claridge Druce approached every plant with the "critical" attitude, especially from the nomenclatural point of view. As a result he created many new names, and accordingly was rebuked by some British botanists for his "contributions to the confusion of nomenclature". This may be so. But there is no doubt whatsoever that no one laboured with more vigour and to more purpose in the interests of British Topographical Botany than this man who began as a poor boy in Northamptonshire and lived to be mayor of Oxford and a Fellow of the Royal Society. For nearly 60 years he travelled the length and breadth of the British Isles, visiting every county, making new records in nearly all of them and compiling Floras of Oxfordshire, Buckinghamshire, Berkshire, Huntingdonshire, Wester Ross and Zetland. Thus no

one made so many county records as Druce, whose knowledge of the plants of the British Isles was unrivalled.

His crowning achievement was *The Comital Flora* (1932) which is really a modern version of *Topographical Botany* but with Ireland included. It did a great service to British topographical botany, for in the course of its compilation, Druce reviewed nearly the whole of British taxonomic botany, using all the records which seemed to him dependable, and giving for each species details as to altitude, habitats, peculiarities, synonyms, world distribution, and the first record as a British plant.

The last twenty-five years have been notable for a fairly intensive exploration of the Inner and Outer Hebrides. Since Lightfoot's visit to Scotland in 1772, some of the Islands had, of course, been botanised. Professor Balfour and Mr. Charles C. Babbington journeyed to Skye, North Uist, Harris and Lewis in 1842. The St. Kilda group of islands have been visited several times since Mr. R. M. Barrington was there in 1883. Likewise, the Island of Barra. In 1894, Mr. W. A. Shoolbred botanised in North Uist, Benbecula, Harris, Taransay and Barra. But, as many of these studies were far from exhaustive, it was obvious that a comprehensive survey of the Hebrides would reveal many new records. That this has been the case is clear from the results of Miss M. S. Campbell's botanising on South Uist, Benbecula, North Uist, Harris and Lewis. More spectacular are the results of the explorations of the staff of the Department of Botany, King's College, Newcastle-upon-Tyne. In 1934, Professor J. W. Heslop Harrison and his colleagues began a study of the biota of the Inner and Outer Hebrides, with the object of writing a comprehensive Flora of these regions. Though the work is still in progress, these botanists have visited the whole of the major islands and many of the less important ones, including Lewis and Harris, Great Bernera and Little Bernera (Lewis), Pabbay, Berneray and Taransay (Harris), North Uist, Baleshare, the Monach Isles, Benbecula, South Uist, Eriskay, Fuday, Fiaray, Barra, Vatersay, Flodday, Muldoanich, Sandray, Pabbay (Barra), Mingulay and Berneray (Barra).

These investigations have resulted not only in an extraordinary extension in the range of some species, especially arctic-alpine species, but also in the addition of several new species to the British flora. Perhaps the most interesting of the latter is

Potamogeton epihydrus from South Uist, its discovery there providing an additional member of the American element in our flora. North and South Uist also have yielded new Scottish localities for another American species, *Najas flexilis*, and both second stations in Scotland for *Eriocaulon septangulare* and *Spiranthes romanzoffiana*. Thus a second centre of distribution of American species has been established in the Hebrides. On the mountains of Rhum, where Lightfoot found so many interesting alpine, *Thlaspi calaminare*, new to Scotland, has been located. Here also the third station for *Arenaria norvegica* in Scotland was discovered, this plant previously being known only from West Sutherland and Shetland although more recently a fourth station has been found in Westernness. From the same mountain group on Rhum three sedges new to Britain have also been reported. Two other Hebridean discoveries worthy of special mention are *Orchis majalis* var. *occidentalis* which is new to Scotland and *Potamogeton rutilus* on North Uist which elsewhere in the British Isles occurs only in Shetland.

Two further important additions to the flora of the Western Islands must be recorded. First the finding in 1934 by Mr. H. M. and Dr. Mountfort of *Koenigia islandica* near The Storr, Skye (though the real identity of the plant was only made known in 1950 by Mr. B. L. Burtt) and again on Mull by Mr. R. W. M. Corner in 1956, and secondly the discovery in South Uist in 1956 by Dr. D. H. N. Spence of *Homogyne alpina*.

These are but a few of the results, the more exciting ones it is true, of this intensive exploration of the Hebrides. It must be remembered that Rhum, for instance, has now been combed by botanists at nearly all seasons of the year, otherwise several of the plants would never have been recorded. How easily they may be overlooked can be gauged from the fact that, because they are present in such exceedingly small quantities, it is possible to go to the spot where one knows a particular plant to grow and only locate it after very exhaustive search. Compared to Rhum, many mountains on the Scottish mainland are botanically unexplored and the fact that Rhum is so rich in rare arctic-alpine suggests that some of these unexplored mountains will also reveal their treasures to intense botanical study. This suggestion has been strongly substantiated during the past few years by the discovery of *Artemisia norvegica* var. *scotica* in 1950 by Sir

Christopher Cox near Ullapool, Wester Ross; of *Diapensia lapponica* near Glenfinnan, Inverness-shire, by C. F. Tebbutt in 1951; of *Saxifraga cernua* in the Glencoe area in 1949 by E. C. Wallace and P. R. Bell and on two mountains in the Ben Nevis area in 1956 by E. A. Blake; and by the refinding in 1951, by A. A. P. Slack, of *Homogyne alpina*, where Don claimed to have gathered it—in the parish of Cortachy and Clova.

In spite of MacGillivray's pioneer study of British Mountain vegetation (1832), interest in the Scottish Mountain Flora still remained definitely floristic rather than ecological in its bias. There were, however, one or two important exceptions—the studies of R. Smith on North Perthshire and of his brother, W. G. Smith, on Forfar and Fife, and of Crampton on the vegetation of Caithness. In fact, W. G. Smith's work was largely the basis for the account of the arctic-alpine vegetation in Tansley's standard work on British vegetation in 1938. But the stimulus which the Smiths gave to the study of Scottish Mountain vegetation somehow has failed to infect others and there are still great tracts of mountainous country awaiting detailed vegetational study. It may be that the Nature Conservancy, as well as the newly formed Alpine Botanical Section of the Botanical Society of Edinburgh, will fill in many of the gaps in our knowledge.

CROP IMPROVEMENT AND PROTECTION SPONSORED BY THE STATE IN SCOTLAND.

By C. E. FOISTER

(Department of Agriculture, East Craigs, Edinburgh).

The State for many decades has sponsored crop improvement by administrative procedures including subsidies and other forms of financial assistance but only within recent years has it directly given technical assistance. In 1723, the Scottish "Society of Improvers in the knowledge of Agriculture", realising that agriculture was in a bad way, initiated an advisory service and sponsored technical advance in various ways, including the breeding of new varieties as well as the control of diseases and pests, although knowledge of the latter was very elementary at that time. This scheme forecast the educational and advisory services of the present day but came to an end with the outbreak of the Jacobite rising of 1745. Much interesting material must necessarily be omitted from this brief survey which will deal with some of the technical means used by the State to improve and protect our crops. Although Forestry is briefly referred to, the term "crop" as used here generally means agricultural and horticultural crops. In most cases also the use of the word "State" in practice means nowadays the Department of Agriculture for Scotland.

CROP IMPROVEMENT.

Two aspects of the problem of improvement of crops are varietal purity and the use of higher-yielding types suited to particular agricultural and geographical conditions. In the second half of the nineteenth century the purity of agricultural and horticultural crops was so poor that both the trades interested and the Government of the United Kingdom realised something had to be done to make it possible for purchasers of planting stock to have some guarantee that what they were buying was indeed what they required. Emphasis was given to this in the case of potatoes, when the outbreaks of Wart Disease (*Synchytrium endobioticum*) just prior to 1914 made it imperative, as new immune varieties became available, that a variety sold as

immune from the disease was not mixed with susceptible varieties. Also certain varieties of horticultural and agricultural crops were prone to give a low yield, and an admixture of different types therefore reduced the potential yield capacity of the named varieties grown. Further, some varieties of crops were not only more susceptible to infection with both fungus and virus diseases but could carry some of the diseases without symptoms although crop yield was still reduced. This made it difficult to be certain that a crop was substantially virus-free and made roguing for that purpose almost an impossibility.

It was at this point that the State intervened directly in order to overcome a number of these difficulties. In 1913 the Department of Agriculture for Scotland (then the Board of Agriculture) initiated work on seed testing, following the pioneer work which had been carried out in certain European countries, which led to improvements in the standards of true seed passing in national and international trade, with regard to purity, freedom from weed seeds, and better germination. This became consolidated and improved by legislative control in 1920 with the passing of the Seeds Act and successive regulations made under that Act. An Official Seed Testing Station for Scotland was opened at East Craigs in 1925 and now collaborates with two other Official Stations, at Cambridge and Belfast, in maintaining uniform standards of testing, and takes a leading part in the establishment of international standards by its participation in the work of the International Seed Testing Association. The control of seed passing in trade is the only compulsory method of crop improvement used by the State, although, as will be seen later, quite a number of compulsory measures concern crop protection.

The Department of Agriculture, however, have initiated several voluntary schemes for crop improvement. The first of these, a potato inspection and certification scheme for wart-immune varieties, was started in 1918 when purity was the only consideration. Later, a very small acreage of selected potato plants was grown in isolation, the selected plants having been judged solely by visual symptoms to be virus-free, and when bulked up these stocks were shown to be a great improvement on the general run of commercial stocks at that time. The scheme grew and has been improved in very many ways, especially since 1932 when standards of health were steadily raised, and again

since 1945 when the production of virus-tested material was initiated. Up to a few years ago there were four different grades of seed, the lowest grade receiving B reports, followed by H, then A, then SS (Stock Seed started in 1922) certificates. No B reports are now issued and seed of H certificated crops may not be offered for further inspection and can only be sold for seed purposes outwith Scotland or for ware purposes. The present aim is to feed into the seed trade tested stocks of the very highest quality of type and health (i.e., V.T. stocks (virus-tested), F.S. stocks (Foundation Seed) derived from V.T. stocks), these stocks either being supplied directly from the Department of Agriculture's propagation centres or by private raisers. By this means it is hoped substantially to eliminate most of the virus diseases of potatoes which cause serious and regular loss of crop; it has been proved that there is a limit to the improvement which can be made by selecting, solely by visual inspection, plants from crops which are known to be virus infected. The present acreage (1957) of the different grades of certificated potato seed is given below, and shows the importance of this part of Scotland's agriculture, especially when it is realised that an average of over 291,000 tons of seed potatoes are sold to England and Wales annually, and approximately 20,000 tons of seed are exported.

<i>V.T.</i>	<i>F.S.</i>	<i>S.S.</i>	<i>A.</i>	<i>H.</i>	<i>Total</i>
79½	2,283½	4,580	50,332¾	15,439½	72,715 acres

Similar certification schemes aimed at the improvement of health and the elimination of impurities are operated by the Department for oats (started in 1950), blackcurrant (1929), raspberry (1930), strawberry (1936) and shallots (1947). The introduction of an oat certification scheme after the last war was intended to replace the registration (see later) of oat varieties since it was felt that this might achieve more to improve the purity and health of commercial oat crops, particularly those grown for seed purposes, than by registration. By limiting inspection to certain varieties of oat, it is hoped to increase the production of varieties of greater merit for Scottish conditions. In 1957, 85 stocks of oat varieties totalling 3,675 quarters of seed were certified as "Stock Seed" and 191 crops totalling 2,278 acres were granted "growing crop" certificates. While this acreage is not yet large, it should be emphasised that these certificated stocks

lead to an improvement in the general oat crop standards much as V.T. and F.S. stocks of potatoes lead to improvement in the purity and health of potatoes. The value of such a scheme will be appreciated when it is realised that the oat crop is a major one in Scotland comprising 819,000 acres producing approximately 816,000 tons of grain, 60,000 tons of which passes through the Scottish "seed" trade and some 40,000 tons exported to England. In the case of the raspberry and strawberry certification schemes there are a number of grades of certificate, the highest of which are granted to crops which are substantially virus-free, having been produced from virus-tested material raised either by the Scottish Horticultural Research Institute or by East Malling Research Station in Kent.

The Department of Agriculture also have another method for improving crop quality and yield, namely the registration of new varieties which on test achieve a required standard at least equal to the best of the established varieties of the crops concerned. A scheme for the registration of agricultural plants was started in 1917, and by 1921 potato registration was introduced. However, there is at the moment no intention to apply registration to crops other than potato. In this scheme new potato varieties, raised either by private breeders or by official bodies such as the Scottish Society for Research in Plant Breeding, are tested over a period of three years not only at the Department's Station at East Craigs but at a number of other centres. The features which are considered are yield, shape, colour, cooking quality, the rate of bulking and the period of maturity of the tubers, the growth character of the foliage and resistance to a number of diseases including wart disease, blight, dry rot, skin spot, gangrene and leaf roll virus. Very few seedling varieties succeed in getting through the complete three years' test and sometimes a variety is carried over for a fourth year. Some of the varieties which have been registered and which are still being grown commercially are: Arran Banner (1927), Arran Consul (1925), Arran Peak (1935), Arran Pilot (1930), Chancellor (1952), Craigs Alliance (1948), Craigs Royal (1947), Dunbar Rover and Dunbar Standard (1936), Gladstone (1934), Orion (1947), Pentland Ace (1951), Pentland Beauty (1955), Redskin (1934) and Vanguard (1939). Soon after the potato scheme was started consideration was given to the testing and registration of commercial oat varieties of that

time. Some varieties were tested at East Craigs and elsewhere but resistance to diseases or pests was not considered and only three, namely Bell, Early Miller and Elder, were registered, the scheme being dropped on the outbreak of war in 1939.

Yet another method is available to improve the quality and yielding capacity of crops and is applied to certain grasses grown for special purposes such as Ryegrass, Cocksfoot and Timothy. In association with the National Institute of Agricultural Botany and the Scottish Agricultural Colleges, single-spaced plant trials at East Craigs and sward trials at the three Colleges have been conducted since 1951 and reports are published on these at regular intervals so that commercial growers can have information on the potential uses and merits of certain varieties of these three grasses in certain districts and agricultural conditions.

The above schemes are carried out directly by the State, but the State also sponsors indirectly the improvement of a number of crops by providing financial and other support for advice in crop husbandry and for experimental work at the three Scottish Agricultural Colleges. Fundamental work is carried out at the research institutes in Scotland under the aegis of the Agricultural Research Council, the financial control being administered by the Department of Agriculture. These institutes are the Scottish Society for Research in Plant Breeding, the Scottish Horticultural Research Institute and the Macaulay Institute for Soil Research. A further development in crop improvement is in forestry where the recently-formed Scottish Forest Tree Seed Association aims at encouraging the use of seeds and plants of the best known origins and, where suitable, prime woodlands are selected and registered as "Approved Seed Sources".

CROP PROTECTION.

In 1877 the Government introduced the Destructive Insects and Pests Act because of the fear that potato Colorado Beetle might be introduced into this country from Europe, where this pest had arrived from America in the late nineteenth century and was causing such havoc as to indicate that its arrival in this country might ruin production of potatoes both for seed and ware purposes within a short time. Amending Acts appeared in 1907 and 1927, these two Acts mainly giving powers to deal with any non-indigenous pest or disease in addition to Colorado Beetle.

While a number of diseases and pests have found their way into this country in the years soon after the passing of these Acts, nevertheless many diseases and pests have been successfully excluded. Some of these are such as Colorado Beetle, San José Scale, Japanese Beetle, Grand Rapids Disease of tomato (*Corynebacterium michiganense*), Bacterial Ring Rot of potato (*C. sepe-donicum*) and Rose wilt (virus). The Department of Agriculture along with the Ministry of Agriculture, Fisheries and Food collaborates with the Forestry Commission in legislating for the control of non-indigenous diseases and pests of forest trees and, on the advice of the Commission, various Importation of Forest Trees (Prohibition) Orders, the last being issued in 1952, are made to prohibit certain forest trees, the introduction of which involve special risks in introducing diseases and pests such as Elm Phloem Necrosis disease (virus) and Chestnut Canker. It is not enough, however, to protect this country from the introduction of non-indigenous diseases and pests, and in order to safeguard both the grower and the purchaser of planting stocks, principally of horticultural material, a Sale of Diseased Plants (Scotland) Order was first introduced in 1922 and totally revised in 1936. This Order, along with amending legislation enacted since that date, prohibits the sale of planting material substantially infected with certain diseases and pests. Examples are Club Root on seedling brassicas, American Gooseberry Mildew, Fruit Tree Cankers, bulk diseases and pests, Woolly Aphis, scale insects and onion smut. It was in order to have a scientific background to this legislation to protect plants from the effects of diseases and pests that a Plant Pathology Laboratory was established in Edinburgh in 1924 and later combined with Entomology, Nematology, Seed Testing and Plant Registration to form the present Scientific Services of the Department of Agriculture for Scotland.

The growing menace of Colorado Beetle on the European Continent and the attempt to plan measures against it by several countries acting together led to the formation in 1951 of the European and Mediterranean Plant Protection Organisation of which the United Kingdom is a member. This regional organisation convenes working parties of specialists to advise member governments on legislative and technical action which can be taken on a uniform basis to control specific crop pests and

diseases, seed-borne diseases, food infestation and musk-rats. Several attempts have been made over the last forty years to organise plant protection measures internationally so that legislation for plant health reasons would only be enacted when justified on scientific grounds and would be so formulated to disturb international trade to the minimum degree. The most successful agreement has been that formed in 1951 under the aegis of F.A.O. and known as the International Plant Protection Convention; the United Kingdom ratified their acceptance of the Convention in 1953. One of the conditions of the International Plant Protection Convention is that measures shall be taken to organise plant protection services of an exporting country so that a certificate which is issued with exported planting material has a sound basis. Importing countries should be able to trust the word of an exporting country whose plant protection organisation is efficient. Each country makes its own plant quarantine regulations which may prescribe that consignments must be completely free from certain diseases and pests and are otherwise substantially free from any other diseases and pests which are not specifically prescribed. Another condition of the Convention is that countries shall take reasonable measures to control the diseases and pests of their crops and, further, should gather and publish information on the more important diseases and pests and their distribution and control. For all these purposes the Department of Agriculture for Scotland has to provide scientific personnel with the necessary laboratory facilities and a well trained body of inspectors, some of whom are agricultural specialists and others horticultural. Although this survey does not deal with work that is being carried out to help the farmer and the country at large to control vermin or other destructive animals, such as rabbits, rats, mice, voles and squirrels, the fact remains that these have to be kept in mind as well as the normally less readily recognised pests and diseases of crops.

Another aspect of plant protection became important in the "thirties" when crop protection products such as fungicides and insecticides became much more numerous. Some were of doubtful value and in association with the chemical industry, the Ministry of Agriculture initiated discussions which later in 1942 led to the formation of a Crop Protection Products Approval

Scheme in association with the Department of Agriculture for Scotland; this made it possible for manufacturers of fungicides and insecticides (and, later, herbicides) to apply for approval of their products. The scheme is administered from the Plant Pathology Laboratory of the Ministry of Agriculture, Fisheries and Food at Harpenden. For the purposes of approving these products an Advisory Committee of experts assesses the evidence on the biological efficacy of the products, on their physical and chemical composition, and on the absence of danger to user as well as to the crop. Owing to the increasing toxic hazard of some of the more recent insecticides and a smaller number of fungicides, the Government convened a series of working parties which considered the possible danger of these products to the user, consumer and wild life, and later formed an Inter-Departmental Advisory Committee on toxic hazards in which the Departments of Agriculture and Health and the Home Office are represented. It is assisted by a technical sub-committee which, with the goodwill of the manufacturers concerned, adjudicates on the toxic hazards of all modern crop protection products likely to come on the market.

Lastly, the State indirectly assists in crop protection in a more general way by financing the advisory services, a part function of which is to identify weeds, diseases and pests affecting crops and to give advice to the agricultural and horticultural growers on methods of control. In Scotland this service is given by the three Scottish Colleges of Agriculture, each of which is autonomous. However, the Department of Agriculture for Scotland sponsors and shares in conferences of specialist advisory officers to discuss current problems in crop protection, and joint action on any of the problems raised.

It will thus be seen that the State intervenes on a legislative basis to a minor degree but achieves many useful results in crop improvement and crop protection by means of voluntary schemes and by the provision of research and advisory services covering the whole field of agricultural and horticultural production.

AN EVOCATIVE HABITAT.

By H. B. GILLILAND

(Department of Botany, University of Malaya).

The range of pitcher plants in Malaya is dealt with in a general sense by Holttum (1954a). He draws attention to the widespread lowland forms and to the fact that the high mountain species tend to be more restricted in distribution. At the present time, on the island of Singapore, the species and their hybrids characterise man-disturbed sites, usually with the "pioneer" and the "*Adinandra belukar*" (Holttum, 1954b; Gilliland, 1956, 1957) stages in occupation. *Nepenthes ampullaria* can survive into the *Arthrophyllum-Anisophyllea* stage. Undisturbed sites on the island, where these interesting plants grow, are now rare.

However, in neighbouring Borneo a community was encountered recently, of which *Nepenthes* spp. might be said to be characteristic, and which, though possibly burnt fortuitously in the fairly recent past, had not been disturbed in the sense of either felling for timber or use for agriculture.

The Forest Service in Sarawak has recently established a National Park at Bako, at the mouth of the Kuching River, opposite the famous mountain, Santubong (Beccari, 1904). The Director of the Botanic Gardens, Singapore (Mr. J. W. Purseglove), undertook to collect specimens of the plants growing in this National Park, and to arrange for their identification. For this purpose he made two visits to the Park and, on the second, I was able to accompany him, and to make population studies on the "padang" on Bako, these studies revealing the community referred to here.

"Padang" vegetation has interested botanists in Malaysia for a considerable period (see van Steenis, 1935, for a summary of descriptions and views). "Padang" vegetation is distinguished primarily by the presence of certain characteristic plants, e.g. *Baeckia*, *Dacrydium* and *Drosera* and produces an impression on the eye of the observer, relative to the more normal forest, similar to that produced by moorland in Europe. The "padang" at Bako has developed upon the surface of a sandstone block, many acres in extent, dipping slightly to the north-west, adjacent to and

north of the Rest House. The rock is exposed in several places and, where soil has developed, it is very shallow and readily water-logged. The major community which has developed has a society of *Ploiarium-Cratoxylon* in the centre with, round the margin particularly to the west, a *Baeckia-Dacrydium* society. Analysis of these two societies are presented as Tables I and II respectively (see Gilliland, 1952, 1956, 1957 for technique).

TABLE I

PLOIARIUM ALTERNIFOLIUM "PADANG" COMMUNITY. BAKO NATIONAL PARK: FEBRUARY 1957.

SPECIES	DIAMETER CLASSES				%	Fidelity
	0-1	1-3	3-5	Total		
WOODY PLANTS						
PLOIARIUM ALTERNIFOLIUM	1787	12	3	1802	68.5	10
CRATOXYLON GLAUCUM	538	14	—	552	19.2	10
RHODAMNIA CINEREA	84	1	—	85	2.9	9
PTERNANDRA COERULESCENS	60	—	1	61	2.1	9
WORMIA SUFFRUTICOSA	37	—	—	37	1.2	8
EUGENIA TETRAPTERA	10	—	—	10		5
MELASTOMA MALABATHRICUM	6	—	—	6		3
MYRICA ESCULENTA	6	—	—	6		3
PLEIOMELE SP.	5	—	—	5		3
STYPHELIA MALAYANA	5	—	—	5		2
GAERTNERA BORNEENSIS	1	—	—	1		1
TIMONIUS SP. I	1	—	—	1		1
TIMONIUS SP. II	1	—	—	1		1
COMBRETOCARPUS ROTUNDATUS	1	—	—	1		1
BAECKIA FRUTESCENS	1	—	—	1	1.8	1
CASUARINA SUMATRANA	1	—	—	1		1
XYLOPIA MALAYANA	1	—	—	1		1
GLOCHIDION BRUNNEUM	1	—	—	1		1
TETRAMERISTA CRASSIFOLIA	1	—	—	1		1
XANTHOPHYLLUM CF. AMOENUM	1	—	—	1		1
XANTHOPHYLLUM CF. WRAYI	1	—	—	1		1
8 UNKNOWN SPECIES	8	—	—	8		1 each
Totals	2557	27	4	2588		
CLIMBERS						
NEPENTHES GRACILIS	167	—	—	167	5.8	10
NEPENTHES RAFFLESIANA	59	—	—	59	2.1	7
FLAGELLARIA INDICA	46	—	—	46	1.6	9
TETRACERA AKARA	19	—	—	19		7
ALYXIA FORBESII	2	—	—	2		2
PSYCHOTRIA SARMENTOSA	2	—	—	2		2
Totals	295	—	—	295	100.00	

OTHER HABITS.

Epiphytes: *Hydnophytum formicarium* (8)*; *Dischidia rafflesiana* (8); *Phymatodes sinuosa* (4); *Myrmecodia tuberosa* (3); *PACHYCENTRIA GLAUCA* (7); *DISCHIDIA GAUDICHAUDII* (9); *BULBOPHYLLUM SP. I* (5); *BULBOPHYLLUM SP. II* (1); *APPENDICULA SP.* (1).

Parasites: *LORANTHUS SP.* (3); *HENSLOWIA BUXIFOLIA* (1).

Herbs: *LYCOPodium CERNUM* (10); *ISACHNE CONFUSA* (10); *RHYNCHOSPORA SP.* (9); *SCHOENUS CAELOSTACHYS* (8); *BROMHEADIA FINLAYSONIANA* (8); *GLEICHENIA LINEARIS* (7); *SELLIGUEA HETEROCARPA* (5); *XYRIS BORNEENSIS* (5); *BURMANNIA DISTICHA* (5); *Utricularia racemosa* (3); *HEDYOTIS SP.* (2); *Drosera spathulata* (1); *LYCOPodium CAROLINIANUM* (1); *SPATHOGLOTTIS MICROCHILINA* (1); *CLADIUM UNDULATUM* (1).

*Figures in parenthesis give fidelity. Species in italics are myrmecophilous or insectivorous.

TABLE II
ROCK MARGIN COMMUNITY: "PADANG" ON BAKO: SARAWAK:
FEBRUARY 1957.

A. FIDELITY 6 OR MORE	DIAMETER CLASSES					%	Fidelity
	0-1	1-3	3-5	5-7	Total		
TREES							
DACRYDIUM ELATUM	50	11	6	1	68	2.2	9
CASUARINA SUMATRANA	12	9	6	2	29	.9	7
CRATOXYLON GLAUCUM	528	52	4	—	584	18.9	10
PLOIARIUM ALTERNIFOLIUM	418	47	5	—	470	15.3	9
COMBRETOCARPUS ROTUNDATUS	57	7	1	—	65	2.1	9
MYRICA ESCULENTA	47	1	2	—	50	1.6	10
EUGENIA TETRAPTERA	359	6	—	—	365	11.8	10
RHODAMNIA CINEREA	284	17	—	—	301	9.8	10
PTERNANDRA COERULESCENS	29	2	—	—	31	1.0	7
PARASTEMON UROPHYLLUM	27	2	—	—	29	.9	8
Totals	1811	154	24	3	1992	64.5	—
SHRUBS							
STYPHELIA MALAYICA	250	—	—	—	250	8.1	10
WIKSTROEMIA INDICA	93	—	—	—	93	3.0	9
EUTHEMIS ENGLERI	48	—	—	—	48	1.5	9
WORMIA SUFFRUTICOSA	18	—	—	—	18	0.5	6
Totals	409	—	—	—	409	13.1	—
CLIMBERS							
NEPENTHES RAFFLESIANA	105	—	—	—	105	3.4	8
NEPENTHES GRACILIS	34	—	—	—	34	1.2	6
NEPENTHES ALBOMARGINATA	16	—	—	—	16	0.5	6
ALYXIA FORBESII	94	—	—	—	94	3.0	10
TETRACERA AKARA	41	—	—	—	41	1.3	10
Totals	290	—	—	—	290	9.4	—



1. *Nepenthes albomarginata* in the society analysed in Table II.



2. *Myrmecodia tuberosa* on *Cratogeomys* in the society analysed as in Table II. *Dischidia gaudichaudii*, with its opposite hemispherical leaves, is seen creeping on the trunk.

B. FIDELITY 5 OR LESS

TREES

WHITEODENDRON							
MULTONIANUM	115	1	1	1	118	2	
BAECKIA FRUTESCENS	37	1	—	—	38	4	
CALOPHYLLUM (large leaf)	22	1	—	—	23	4	
CANTHIUM sp.	13	2	—	—	15	4	
TRISTANIA sp.	—	1	—	—	1	1	
XYLOPIA MALAYANA	—	1	—	—	1	1	
GARCINIA sp. I	11	—	—	—	11	4	
GARCINIA sp. II	9	—	—	—	9	5	
GARCINIA sp. III	9	—	—	—	9	4	
ORMOSIA sp.	3	—	—	—	3	2	
EURYCOMA LONGIFOLIA	2	—	—	—	2	2	
GUIOA sp.	2	—	—	—	2	2	

Totals	223	7	1	1	232	7.5	—
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SHRUBS

GAERTNERA BORNEENSIS	15	—	—	—	15	5	
CALOPHYLLUM (small leaf)	8	—	—	—	8	5	
TIMONIUS sp.	5	—	—	—	5	3	
EUGENIA sp.	3	—	—	—	3	3	
ELAEOCARPUS sp.	1	—	—	—	1	1	

Totals	32	—	—	—	32	1.0	—
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CLIMBERS

HENSLOWIA UMBELLATA	15	—	—	—	15	4	
FLAGELLARIA INDICA	8	—	—	—	8	4	
GNETUM sp.	3	—	—	—	3	2	
PSYCHOTRIA SARMENTOSA	3	—	—	—	3	2	

Totals	29	—	—	—	29	0.9	—
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UNKNOWN	100	—	—	—	100	3.2	—
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OTHER HABITS.

Epiphytes: *Hydnophytum formicarium* (10); *Dischidia rafflesiana* (10); *Myrmecodia tuberosa* (9); *Phymatodes sinuosa* (7); *DISCHIDIA GAUDICHAUDII* (10); *PACHYCENTRIA GLAUCA* (10); *BULBOPHYLLUM* SP. (9); *APPENDICULA* SP. (6).

Parasites: *LORANTHUS* SP. (6).

Herbs: *RHYNCHOSPORA* SP. (10); *BROMHEADIA FINLAYSONIA* (9); *SCHOENUS CAELOSTACHYS* (9); *CLADIUM UNDULATUM* (8); *LYCOPODIUM CERNUUM* (7); *GLEICHENIA LINEARIS* (7); *ISACHNE CONFUSA* (6); *Utricularia racemosa* (4); *BURMANNIA DISTICHA* (4); *XYRIS BORNEENSIS* (3); *SELLIGUEA HETEROCARPA* (3); *SCLERIA* SP. (3);

Notes: PLOIARIUM ALTERNIFOLIUM = ARCHYTAEA VAHLII of earlier authors. Specimens (under J. W. Purseglove's collecting numbers) on which determinations are based are housed in the Herbarium, Singapore Botanic Gardens.

The first society, with a total of 7.9% of *Nepenthes* spp. recorded out of a total count of 2,883 woody plants and climbers and moreover with the two species having a fidelity of *N. gracilis* (10) and *N. rafflesiana* (7) respectively, has also in its ground flora of herbs the characteristic *Drosera* (*D. spathulata*) and *Utricularia racemosa*, a further carnivorous plant.

In the second society, although *Drosera* is not present, three species of *Nepenthes* occur with again a high percentage occurrence, 5.1% out of a total of 3,084 woody plants and climbers, and with a high fidelity of *N. rafflesiana* (8), *N. gracilis* (6) and *N. albomarginata* (6). Here again *Utricularia racemosa* is present.

Equally remarkable are the number and constancy of the myrmecophytes. In the first society, four undoubted myrmecophytes are recorded, two of high fidelity, while in the second the same four occur, all in this case with a high fidelity. The myrmecophyte symbiosis has excited interest ever since Beccari's account (1877-90), and an adequate explanation of the plant's benefit from the ant partners has not yet been provided. The suggestion that the plant derives nitrogen supplies from the ant's excreta (Beccari, 1904) appears to be the most satisfactory in the present state of our knowledge. It is doubtful whether *Pachycentria glauca* is a myrmecophyte in the strict sense, for no cavities housing ants were found in any of a large number of specimens examined.

Such examinations of roots as have so far been carried out have not disclosed mycorrhiza or root nodules, but Bond's recent (1957) demonstration of root nodules on *Casuarina* is significant.

The number of different plants with highly specialised structures clearly rules out coincidence as an explanation of their presence; it would seem rather to indicate their joint ability to deal with a feature of the habitat to which the majority of unspecialised plants are not adapted.

Bako enjoys a humid tropical climate with a non-seasonal rainfall distribution and a minimum temperature in excess of 70° F. It would be reasonable to expect, therefore, a Tropical



3. *Hydnoophytum formicarium* on *Cratoxylon*, showing the tuber opened to reveal the ant corridors.



4. *Dischidia rafflesiana* on *Cratoxylon* showing heavily invaginated leaves which are ant-inhabited, and the detritus in which *Dischidia* ins its own roots.

Rain Forest to be present (Richards, 1952) and, indeed, this is the vegetation of much of the surrounding country.

The climate implies a continual drain on the resources of the habitat with no recuperative winter or dry season. Taken together, all these indications point to a habitat characterised by a nitrogen shortage. Nitrogen (protein) shortage in the humid tropics is such a widespread phenomenon that this is not surprising. The proximal cause in this case must lie in the poor-ness of the rock from which the soil derives—sandstones notoriously produce poor soils.

As noted above, the “padang” vegetation is widespread in Malaysia. From van Steenis’s account above quoted, it is clear that the only disturbing factor is fire, and there is some doubt whether fire is inevitably associated with this vegetation type. Certainly there is no indication that it is secondary in the sense that it follows human disturbance. The evidence of burning found at Bako was of some significance, for this rested upon charred stumps and sticks of *Ploiarium* in situ, from which fresh *Ploiarium* stems had coppiced. From this may be drawn the conclusion that the fire had not altered the main structure of the community. In this sense, then, the community at Bako could be regarded as primary. If that can be accepted then we may regard the sandstone rock, from which the scant soil is developed, as the primal cause of this community. It is relevant to note that elsewhere in Sarawak there are vast areas of peat developed in sites with impeded drainage. The peats are of considerable depth and usually carry forest, not “padang”.

It is not suggested that a parent rock of sandstone leading to a poor soil is the only kind of cause in this climate which could produce a nitrogen-deficient habitat; other causes may well operate. It is, on the other hand, a matter of some interest to reflect that, in the course of geological time, this habitat, with its accentuated feature of nitrogen shortage, is unlikely to have preceded the first emergence of sandstone rock in a humid tropical climate. Sandstones in the Bako area are held to be of Miocene age, while sedimentary rocks of Carboniferous age occur near Kuching (Geol. Survey, 1955).

In the course of a discussion of what Lamarck really said, Cannon (1957) rightly emphasises that the central part of the whole hypothesis, which has so often been wrongly represented,

is the law (the second presented in the *Histoire Naturelle des Animaux sans Verèbres*, 1815), which states the need of a new organ leads to its appearance.

Hardy (1957), in the discussion following Cannon's paper, put the situation into modern terms thus: "The gene complex is varying slightly in almost every direction; if an animal changes its habitat, sooner or later there will be a new gene complex which will give a slight structural change better adapted to the fuller expression of this new habit, and so will tend to survive better than the old one, if the new habit is an advantageous one. For example, if birds of a particular species originally pecked insects off the surface of the bark of trees, but found in a time of shortage that they could obtain more insects by pecking into and under the bark, they might develop a change of habit which might spread through the species, just as we have seen the habit of opening milk bottles spreading through the tit populations of Europe".

To the field botanist considerable interest lies in the new situation in which the organism finds itself, in order that the "need for a new organ" should arise. What are the kinds of new situations which may arise and being in their train a new need? Can one, by examining a situation with unusual characteristics, estimate the kind of change which produced the new need in the past?

This question is one which has exercised the minds of botanists on many occasions, at any rate by inference if not directly so expressed. Bews (1925, 1927); Holttum (1930, 1940, 1955) and Corner (1949, 1954) are examples.

In light of this, may we not suggest that when, during the course of the evolution of the earth, sandstone rocks began to be formed, and to emerge to form land surfaces in the humid tropics, a habitat evocative of devices to supplement the nitrogen available was born, a new need had arisen and the new organ (the carnivorous trap in its various forms) began to appear?

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THE INFLUENCE OF ECOLOGY ON FORESTRY PRACTICE.

By SIR ARTHUR GOSLING

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Long before Ecology was recognised as a scientific study, foresters had been, consciously or unconsciously, applying the results of essentially ecological observations to their work. Line surveys and sample plots (transects and quadrats for the ecologist), laid out to provide information about the composition and yield of forest stands, often furnished much added information about the development of forest vegetation and so led to the elaboration of methods of directing this development. Traditional cutting practices were scrutinised in relation to their effect on seeding and seedling growth and were gradually adapted to meet the needs of the succeeding crop. The fundamental importance of soil moisture and nutrient supply was becoming recognised and the more enlightened European foresters were basing their choice of species in reforestation on field experience of the needs of different trees. In these and many other directions practical forestry was benefiting by the ecological approach and incidentally providing much raw material for the future science of Ecology.

The influence of ecology on forestry practice is effected through the impact of ecological studies and methods on the forester's attitude to the woodland or potential woodland in his charge and thus indirectly on the manner in which his intervention, in the form of planting, cutting and other operations, is exercised (Tansley *et al.*, 1943). Not the least important in this context are ecological studies of the woodland fauna, from the microscopic Arthropoda, which promote the decomposition of acid forest litter, to the larger mammals which inhabit the forest and in some cases threaten its survival. Recent investigations of the biology of the rabbit, the grey squirrel, mice and voles provide good illustrations of the way in which foresters, scientific ecologists and agriculturists have co-operated to the advantage of all. This paper will, however, be restricted to plant ecology and plant succession in their bearing on forestry practice in Britain.

In Britain, as in many other long settled countries where man has been exploiting the native forests for centuries, the greater

part of the forest heritage has vanished. Foresters have therefore often been concerned more with the reforestation of treeless ground than with the management of ancient forests. Until recent years scientific ecology had not, at least in Britain, contributed much to the development of methods used in the afforestation of treeless land. Ecologists had done much useful descriptive work on representative heaths and bogs (Tansley, 1939), but, with few exceptions, little progress had been made in working out the ecology of important wasteland plants, or in studying the communities from the dynamic point of view in relation to changing factors of the habitat. On the other hand some practical foresters, confronted by the difficulties which frequently attend the establishment of trees and observing the very variable results achieved, had attempted to learn from the plant communities occurring naturally on the site and to relate to them, and to the soil properties to which they bore witness, the choice of species and a decision about the need for site amendment. Some early work of this kind was done by Gilchrist (1872) and mention should be made also of the pioneering work of Boyd (1916) in the Crown Forest of Inverliever, Argyllshire. Similarly, in other localities of Britain, where efforts were being made to establish forest on wasteland, foresters were gathering information about the site requirements of different trees; although seldom appearing in print, much of this information was subsequently used on a wider scale.

During the past two or three decades scientific interest in the afforestation of bare land has increased very markedly and ecologists have made important contributions to the assessment and interpretation of site factors and to the building of a framework of knowledge on which a rational choice of species can be made. This increased activity may be due partly to the dynamic approach to the study of plant communities, partly to the widespread interest among botanists in finding out how plants feed, grow and multiply in their natural environments, partly to the conduct by the Forestry Commission of large-scale ecological experiments, involving alteration of the environment and a change in vegetation, and partly to the support given by the Commission to fundamental research which has a bearing on afforestation.

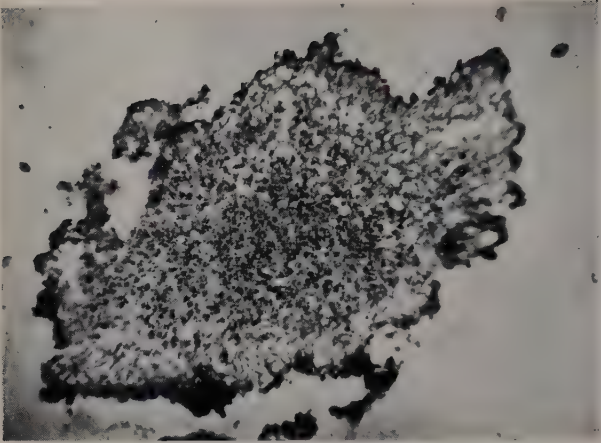
The knowledge, based on historical or archaeological evidence,

or on the results of pollen analysis of peat, that many wastelands bore forest in times past has prompted enquiries into the causes of deforestation and the accompanying changes in soil and subordinate vegetation. The current experimental work of the Forestry Commission in the reforestation of the degraded moorland soils has called forth numerous important investigations by ecologists interested in one aspect or another of this problem. Mention may be made of Rayner's (1944) researches on the mycorrhizal habit in pines in relation to the afforestation of *Calluna* heath in southern England, of Leyton's (1954) studies of the nutritional aspects of tree growth on upland *Calluna* heath, and of Yeatman's (1955) investigation of the relation between root development and successful establishment of trees on ploughed and unploughed heath. Muir and Fraser's (1940) survey of the soil and vegetation of two young forests in Aberdeenshire and Fraser's (1933) studies of Scottish peats in relation to tree growth have had considerable influence in practical afforestation. Dimbleby's (1952, 1958) researches have reminded foresters that their afforestation work, particularly the choice of species, is likely to affect profoundly the development of the soil.

The range of species within which a choice may be made is determined firstly by the climate and secondly by local factors of topography, soil and vegetation. With trees indigenous to the locality, ultimate climatic suitability will not be in doubt, though they may be difficult to establish by planting. But Britain, owing to climatic and geographic changes in Quaternary times, is poor in native timber trees and there is a long tradition of introducing trees from other lands, often with markedly different climates. In many cases such introductions were made for ornamental use in the first instance, but the proof that a tree would remain healthy and grow to large dimensions in an arboretum, park or garden, often led to its extended use in forest planting, at first in the relatively favourable environment of a woodland at moderate altitude.

Accordingly, when foresters were led to employ many exotic trees in wasteland afforestation they had the great advantage of a useful body of information about the tolerance of many species within the British climate and some indication also of the rates of growth to be expected. Initial difficulties and disappointments were mainly due to the inherent defects of the site, which taxed

PLATE I



DIEHLIOMYCES MICROSPORUS.

Fig. 1. T.S. young fruit-body showing central mass of ascogenous hyphae and irregularly arranged asci (showing black owing to deeply stained young ascospores), surrounded by more loosely interwoven sterile hyphae and outer denser but discontinuous peridial layer. ($\times 60$).

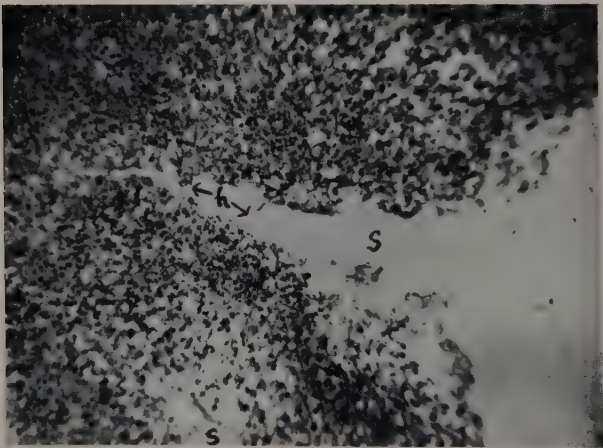


Fig. 2. T.S. part of gleba of mature fruit-body splitting in two places (S), showing hyphae (h) just broken apart. ($\times 60$).

the adaptability of some species well suited climatically. The general mildness of the British winter and the absence of any pronounced dry season are two important factors which have encouraged the planting of trees from other climates, including climates warmer and wetter than ours, and it has sometimes been possible to exploit, with impunity, the faster growth which species from lower latitudes make when planted in Britain. Nevertheless this climate has features which tax the endurance of some of the species which have been tried: for example, the damaging spring frosts, the frequent gales, the constantly high humidity of the western coastal districts, the occasional sharp fall in winter temperature and the cool cloudy summers of the uplands where so much afforestation is carried out.

The variable incidence of these features in Britain and the knowledge that many important exotics have a very wide climatic range has directed attention to the need for more detailed study of some of the species from abroad, which are now being planted on a large scale. Where the species has been examined with some thoroughness within the native range, a good deal of information is available for foresters using the species in Britain. This is most usefully supplemented by study of the tree in its native habitat by foresters familiar with British conditions, as has recently been done for some North West American conifers by Wood (1955) and Day (1957). At the same time, a detailed comparison of climatic data for country of origin with those for Britain indicates which parts of Britain are likely to be most favourable to the tree and from what localities seed should be obtained. Inferences based on these comparative climatic data are tested in provenance experiments, in which plants of diverse seed origins are tried out in a series of uniform environments in different parts of Britain. Such preliminary trials of several geographic forms of the species in the British climate offer a good opportunity of investigating the tree's susceptibility to disease in the changed environment, for it is commonly believed that health and disease are closely bound up with provenance and general climatic suitability. Concurrently, systematic studies of growth and yield and more recently timber properties in existing plantations in Britain provide evidence as to whether the introduced tree is superior to local indigenous species (or, it may be, to alternative exotic species) and define the habitats within which such

superiority is of practical importance. Lastly the influence of the tree on soil development is not the least important of its silvicultural attributes.

In these directions the forester turns to ecological studies for help in the choice of species. He requires both assurance that the species proposed for planting are (in so far as they are not indigenous) suited by the local climate, and some guidance as to how the species climatically suited should be allotted in accordance with features of topography and soil. The forester with an ecological approach has the satisfaction of knowing that plantations created with due regard to significant changes in relief and vegetation are invariably more pleasing to the eye, as well as more successful silviculturally, than those created with wholly artificial boundaries between the species. The influence of pioneer and nurse trees, the effect of drainage and soil cultivation and the action of fertilisers have had some light thrown on them by ecological work and there is clearly wide scope for further work of this kind.

The establishment of healthy productive plantations is nevertheless only the first step in the creation of a forest, with its diverse plant and animal life, in equilibrium with a healthy soil and capable of perpetuating itself. Natural or semi-natural woods are seldom seen in Britain, and where they do occur they have too often suffered serious depletion by past exploitation. Accordingly, it is not easy for British foresters to visualise their artificial plantations, often of exotic trees, as harmonious units of forest vegetation. The problem of finding the best method of managing these artificial woods, with a view to sustained yield, has been exercising the minds of British foresters for some time. On two aspects of the problem there is general agreement, namely that the fertility of the soil must be maintained and that, as the new plantations created in the past 40 years become mature, there will be considerable scope for regenerating them by natural seeding. These two aspects of forestry practice have been strongly influenced by ecological studies.

It is now widely appreciated that a tree's action on soil is compounded of several more or less independent factors, some of which may be modified by silvicultural treatment. The properties in the tree which affect its action on the soil are mainly connected with the chemical composition of its leaves, the charac-

ter, and particularly the depth, of its root system and the local climate under its canopy. The influence of these properties is, of course, dependent on the basic character and evolutionary stage of the soil. It is also dependent in a marked degree on the regional climate. In Britain it is broadly the case that from the point of view of soil improvement the most desirable characteristics of trees are: a litter rich in mineral matter, with a low carbon-nitrogen ratio, and readily attacked by earthworms; a deciduous habit and a canopy of moderate density, which allow warmth to reach the humus layer in spring and early summer and at the same time foster mull-forming ground plants; and an energetic root system, capable of improving the internal drainage of the soil and withdrawing salts from considerable depth. Conversely an acid litter, with high carbon-nitrogen ratio, dense evergreen foliage and a superficial root habit, mark a tree as less desirable from this point of view. With the possible exception of the hazel, no tree excels on every count, but most commercially valuable trees have some points in their favour to offset undesirable traits and the forester will soon be in a position to exploit the favourable properties and to make a rational choice of trees in the light of the local environment of climate, soil and topography.

Where artificial plantations have been created on treeless wasteland the forester faces a somewhat different problem, that of creating or recreating a forest soil on a site which has become degraded under several centuries of moorland vegetation. There is reason to expect that the establishment of a successor stand will be facilitated by the changes in soil and vegetation wrought by the pioneer stand. How far will the expectation of improved yield be realised? How may the action on the soil of the unexact-ing species commonly grown on wastelands (pines and spruces for the most part) be improved by the admixture of species with a richer litter, or by manuring? These and many other ecological problems are presented by current afforestation and it is to be hoped that further research will shed light on them.

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THE DEVELOPMENT OF THE FRUIT-BODY OF DIEHLIOMYCES
MICROSPORUS (Diehl and Lambert) Gilkey
(Syn. PSEUDOBALSAMIA MICROSPORA Diehl and Lambert).

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INTRODUCTION.

The invasion of mushroom beds by a truffle-like fungus was first recorded by Lambert (1930) from the U.S.A. The fungus was described by Diehl and Lambert (1930) as *Pseudobalsamia microspora* and placed in the Tuberales. Gilkey (1954) transferred it to the Eurotiales, under the name *Diehliomyces microsporus*.

The fungus, which is known to mushroom growers as "truffle", has frequently been reported from both Europe and America but no complete account of fruit-body development is available. Abundant material of "truffle" was obtained from a number of places in England and comparison of this with type material of *Pseudobalsamia microspora* showed it to be the same species. Hand sections, freezing-microtome sections and stained serial (microtomed) sections of fruit-bodies at different stages of development were prepared.

DEVELOPMENT OF FRUIT-BODY.

The smallest fruit-bodies examined were more or less spherical and about 1 mm. in diameter. Even these already possessed a central mass of ascogenous hyphae bearing numerous asci, many of which obtained fully developed ascospores. Both ascogenous hyphae and asci were arranged irregularly and there was no sign of an incipient hymenium, such as is seen in *Tuber* spp. The central ascogenous mass was surrounded by a layer of finer hyphae. These were loosely interwoven but formed a rather closer layer at the periphery of the fruit-body. In these young fruit-bodies no sign of either a definite preformed aperture or of any folding of the ascogenous mass could be detected (Plate I, 1; Fig. 1, A).

Individual fruit-bodies reached a size of 1-2 cm. but often a number adhered together to form a crust on the surface of the

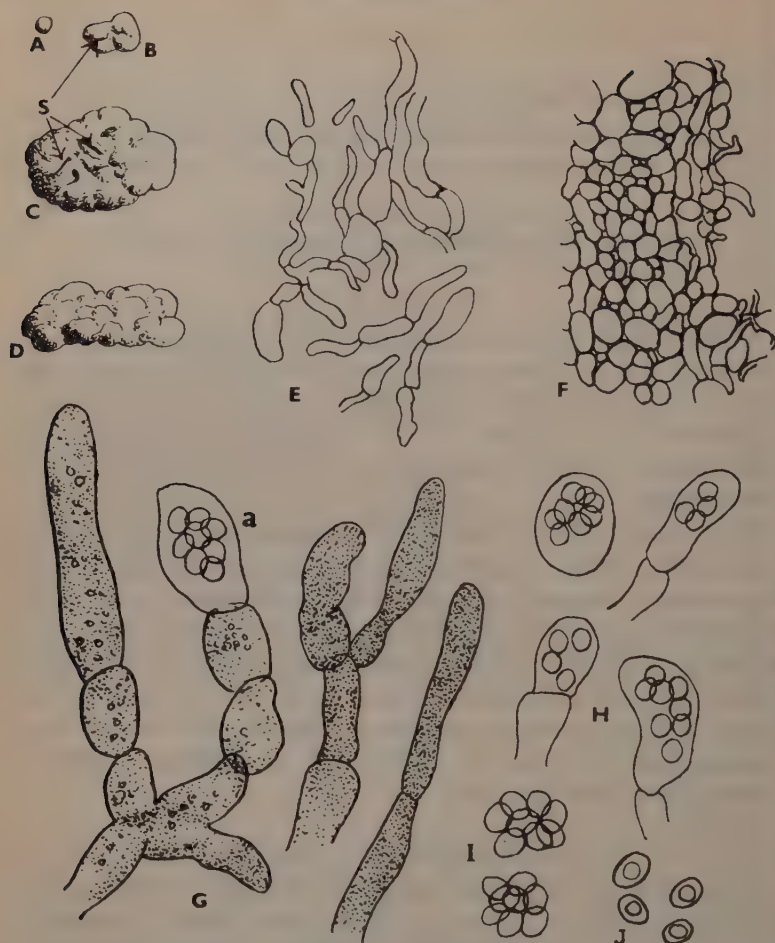


Fig. 1. *DIEHLIOMYCES MICROSPORUS*.

A. Young globose fruit-body. B. Older fruit-body already wrinkled and beginning to split. C. More or less globose mature fruit-body which had grown in loose soil, showing numerous wrinkles and several splits reaching surface (s). D. Crust-like mature fruit-body formed over harder surface. A-D. Natural size. E. Sterile hyphae from zone immediately surrounding central ascogenous mass (drawn from section). F. T.S. outer half of plectenchymatous peridium showing extreme outer edge with irregular torn hyphae with closely packed hyphae underneath. E and F $\times 200$. G. Ascogenous hyphae; older one on left shows dense granular contents and oil drops and one nearly mature ascus; younger one on right shows more slender elongated apical cell. H. Nearly mature asci, including two atypical ones with only four ascospores. I. Groups of ascospores shed from asci. J. Mature ascospores each with single oil drop. G-J $\times 900$.

compost. These larger and presumably mature fruit-bodies were convoluted, usually more or less flattened and sometimes showed variously arranged slits in the peridial layer exposing the ascogenous mass (Fig. 1, B, C, D). The macroscopic appearance suggested that the ascogenous mass might be folded in a manner reminiscent of some of the simpler members of the Tuberales. Microtomed material, however, revealed beyond doubt that the folded appearance was misleading, and that the segmentation of the fruit-bodies was due to the development of more or less radially arranged splits. The ascogenous mass in a developing fruit-body enlarges more rapidly than the external layers and causes tearing of the latter, giving apertures superficially resembling the preformed openings seen in some members of the Tuberales. In many sections the tearing apart of segments of mature fruit-bodies could be clearly seen, with hyphae on opposite sides of the gap matching each other or still actually in contact (Plate I, 2).

STRUCTURE OF MATURE FRUIT-BODIES.

In their original description of this fungus Diehl and Lambert (1930) give details of some of the elements composing the fruit-body. The present observations confirm most of these but the interpretation of the nature of some of them depends upon the method of development of the fruit-body.

Peripheral layers.—In some collections large lumps of soil were present. When these were broken across, they revealed a large fruit-body surrounded by a "crust" of soil bound together by interwoven hyphae and resembling the crust of species of *Elaphomyces*. No such crust surrounding *Diehliomyces* fruit-bodies has been described before.

The layer of sterile hyphae surrounding the ascogenous mass reached a thickness of 1-2 mm. It was composed of branched and anastomosing hyphae, of diameter 7-12 μ , but with some cells inflated to a diameter of up to 25 μ . Contents were sparse. These hyphae were more closely interwoven at the periphery where they tended to form a thin, more or less compact, peridial layer (Fig. 1, E, F).

Ascogenous hyphae.—The young ascogenous hyphae were of similar diameter (ca. 4.5 μ), were more branched than the sterile

hyphae and contained dense, deeply staining cytoplasm. Older cells were inflated and contained numerous oil drops (Fig. 1, G). The ascogenous hyphae occupied the entire central part of the fruit-body and no sterile hyphae could be seen to correspond to the "paraphyses" mentioned by Diehl and Lambert (1930). At no stage in development was there any trace of a regular arrangement of asci and paraphyses, or of either alone, to form a hymenium. The asci were formed terminally on the irregularly branched ascogenous hyphae and no crozier formation could be demonstrated.

Asci.—The asci were very numerous and entirely irregularly arranged. They were thin-walled, hyaline and of irregular shape, probably as a result of the pressure of surrounding cells during development. They varied in size from $12-25\ \mu$ long $\times$ $8-15\ \mu$ broad and usually contained eight ascospores which were shed at an early stage so that the centre of the fruit-body contained numerous free ascospores.

Ascospores.—The spores were hyaline, globose or nearly so, average size $6 \times 5\ \mu$, containing a single oil drop. Young spores were thin walled and stained readily with carbol fuchsin. Older spores had thicker walls which were impermeable to this stain.

SYSTEMATIC POSITION OF DIEHLIOMYCES.

The genus *Pseudobalsamia* of the Tuberales was introduced by Fischer (1907) to include forms with a subglobose ascocarp; having a distinct point of attachment to the mycelium at the base; infolded at the apex with venae externae forming irregular canals which may be filled with hyphae and may converge towards the apex and open to the surface at one or more points; and with globose to elliptical, stipitate asci, irregularly arranged between the veins and containing eight smooth hyaline ascospores.

Diehl and Lambert (1930) recognised that the mushroom bed "truffle" did not entirely correspond to Fischer's description of *Pseudobalsamia* and pointed out that its inclusion in that genus had been criticised by Gilkey in a personal communication. Gilkey (1939) recorded *P. microspora* as a doubtful species and Hawker (1954) similarly considered its systematic position to be doubtful. The transfer to Eurotiales as *Diehliomyces microsporus* (Diehl and Lambert) Gilkey, made by Gilkey in 1954 at the

request of Dr. Diehl, was undoubtedly justified on the basis of the irregular arrangement and evanescent nature of the asci.

The present investigation supports the inclusion of the mushroom bed "truffle" in the Eurotiales by showing that the ascogenous hyphae and asci are arranged in an entirely irregular manner from the earliest stages of development and that the apparent truffle-like folding of the fruit-body is due to splitting as a result of the tension set up by uneven growth. The presence around some specimens of an *Elaphomyces*-like crust is further evidence favouring the inclusion of the fungus in the Eurotiales. It is perhaps intermediate between the Gymnoascaceae, near which it was placed by Gilkey, and the truly hypogeous, and much more highly developed, Elaphomycetaceae.

SUMMARY.

A study of the structure and development of fruit-bodies of *Diehliomyces microsporus*, the so-called "truffle" of mushroom beds, showed that the apparent folding of the ascogenous mass was due to splitting, as a result of tension set up by unequal growth, and that no true folding occurred. This observation supports the transfer of this fungus from the Tuberales to the Eurotiales.

ACKNOWLEDGMENTS.

Thanks are due to various mushroom growers, members of the National Agricultural Advisory Service and others who sent material and information, to the Director and staff of the Herbarium at the Royal Botanic Gardens, Kew, who allowed me to examine type material of *Pseudobalsamia microspora* and to Mr. H. Joyner who took the photographs included in Plate I.

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PERISTOME TEETH AND SPORE DISCHARGE IN MOSSES.

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Apart from the remarkable air-gun of *Sphagnum*, violent discharge of spores in mosses appears to be limited to those species in which vigorous hygroscopic movements of the outer peristome teeth may flick spores out of the capsule. In *Polytrichum* spp., where the capsule has immobile teeth and a poppy-fruit structure, there is no peristome activity controlling spore liberation. In *Funaria hygrometrica*, with its shutter-like peristome, there is control over spore liberation in the sense that spores can escape only under dry conditions when the slits between the outer teeth (united by their tips in a central plate) gape open. In a number of mosses, however, not only do the outer peristome teeth operate to close the mouth of the capsule under damp conditions, but they also by their violent movements on drying bring about active discharge. This type of activity is seen in such genera as *Brachythecium*, *Eurhynchium* and *Mnium*. The matter received attention from morphologists at the end of last century (Goebel, 1895, and Steinbrinck, 1897). I propose in this paper to re-examine the question and to suggest that spore liberation in mosses is a field for future experimental study.

In the first place it may be well to have a fairly detailed picture of the mechanisms involved, and to this end reference will be made mainly to two common mosses: *Eurhynchium confertum* (Dicks.) Milde and *Mnium hornum* Hedw., both very closely similar in peristome structure.

The peristome teeth are derived from a specialised layer of cells forming a hollow cone open at its apex and with its circular base bedded on the diaphragm (Figs. 1 and 2). As the capsule dries during its final stages of maturation most of the thin-walled parenchyma (dotted in Fig. 1) breaks down completely, the only persistent tissues being the operculum (which is duly discarded), the epidermis (which forms the capsule wall), the diaphragm, the peristome, the columella (in a very shrunken state) and the spores (Fig. 3). Except for the spores, all these tissues consist of dead cells. In the peristome layer not only do the cells die, but

they become partially disintegrated, the conical one-celled layer separating into an inner thin sheet of cell-wall material and an outer relatively thick sheet. Each of these conical sheets is variously dissected by the disappearance of regions of unthickened wall which extend from near the apex of the cone towards its base. By the breakdown of these unthickened parts both the inner and outer peristome are cut into teeth (Fig. 4). In the outer peristome dissection extends right to the base thus completely separating the sixteen teeth, but in the inner it ceases considerably short of the base of the cone (Figs. 5 and 6).

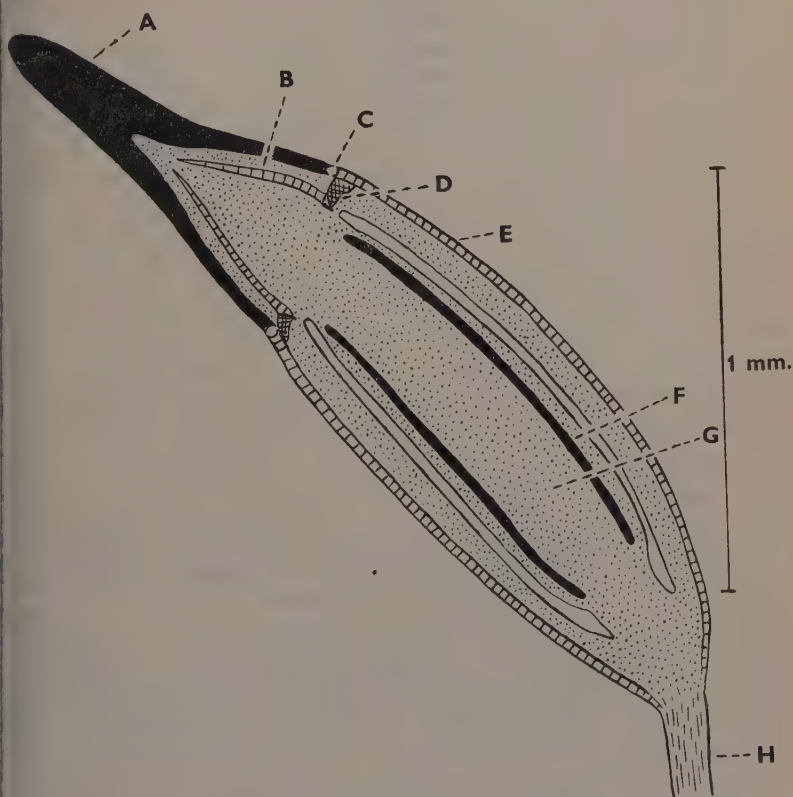


Fig. 1. *Eurhynchium confertum*.

Longitudinal section through an immature capsule. A, operculum; B, peristome; C, annulus; D, diaphragm; E, capsule wall; F, spore sac; G, columella; H, seta. Thin walled parenchymatous tissue is indicated by dotting.



Fig. 2. *Eurhynchium confertum*.

High power details of part of section shown in Fig. 1. A, peristome; B, operculum; C, cells of annulus; D, capsule wall; E, spore sac. Cells of the diaphragm are marked "x".

The heavily thickened outer walls of a single row of cells extending from the base to the apex of the peristome cone constitute an outer tooth. However, it is to be noted that this tooth is essentially a two-ply structure, the inner ply contributed by the outer walls of the peristome cells, the outer one by the inner walls of the layer of cells immediately outside the peristome. The inner peristome is built up by the persistent parts of the inner walls of the peristome layer. Thickening is so distributed, however, that each main tooth of the inner set is derived from two adjacent rows of half cells, the net result being that the inner teeth alternate with the outer. Between the major inner teeth are small thread-like strips of wall material known as cilia.

In sections cut transversely to the long axis of the still intact green capsule in the neighbourhood of the conical operculum the various parts of the final peristome can be seen. These are illustrated for *Mnium hornum* in Fig. 7. In a section near the tip of the capsule (Figs. 7, I and II) the inner peristome teeth are clearly delimited, each being V-shaped in section, the angle representing the line of junction of the two rows of half cells contributing to each tooth. Also the position of the cilia is clearly seen. In *Mnium* there are three between each pair of teeth (Fig. 6). The enormous difference in the thickness of inner and outer teeth is also very obvious. A section further from the tip and nearer the diaphragm (Fig. 7, III and IV) shows the inner peristome as an undissected whole but with very prominent ridges.

If a dry mature capsule of *Eurhynchium*, from which the lid has just separated, is examined under a hand lens, while it is lying on its side on a sheet of glass, the process of violent spore discharge can easily be observed. If one breathes gently on the specimen, thus increasing the humidity, the outer peristome teeth bend inwards through the gaps between the inner teeth depressing the cilia as they do so. It would seem that in this state the capsule is more or less closed, so that spore escape is impossible or at least hindered. An experimental study of this question should be simple. Under damp conditions the tips of the outer teeth in the incurved position become coated with spores from the upper part of the full capsule. On drying, the outer teeth swing rapidly outwards flicking out some spores. Further, as the outer teeth bend backwards their somewhat serrate edges may become momentarily caught on the inner peristome and so

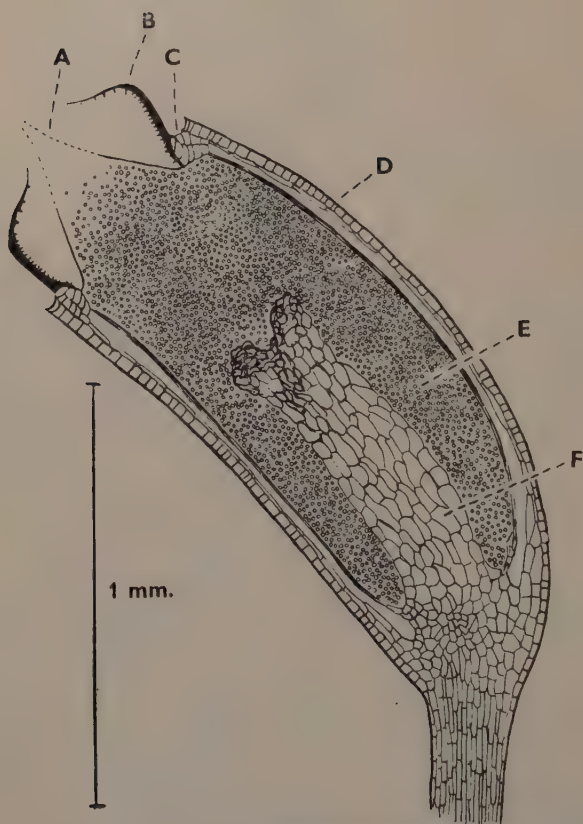


Fig. 3. *Eurhynchium confertum*.

Longitudinal section of a mature capsule with the lid off. A, inner peristome; sectioned part shown by the continuous line, the general outline (not seen in the actual section) indicated by interrupted lines. B, outer peristome tooth; C, diaphragm; D, capsule wall; E, spores; F, columella.

move in a particularly jerky manner. This may also contribute to the violence of discharge even to the extent of jerking off spores adhering to the inner teeth.

At this stage, reference should be made to the structure of the outer teeth in relation to their movement. In *Eurhynchium confertum* each is distinctly two-ply and the microscopic appearance of the two layers is very different (Fig. 8). Movement of the tooth in response to changes in humidity can be explained on the theory that the outer layer is strongly hydrophilic, the inner being not hydrophilic or much less so than the outer. Thus in damp air the outer layer would appear to absorb water and thus increase in length whilst no change occurs in the inner. So the tooth bends inwards. The inner layer is optically fairly homogeneous, but the outer is not so. This consists of numerous

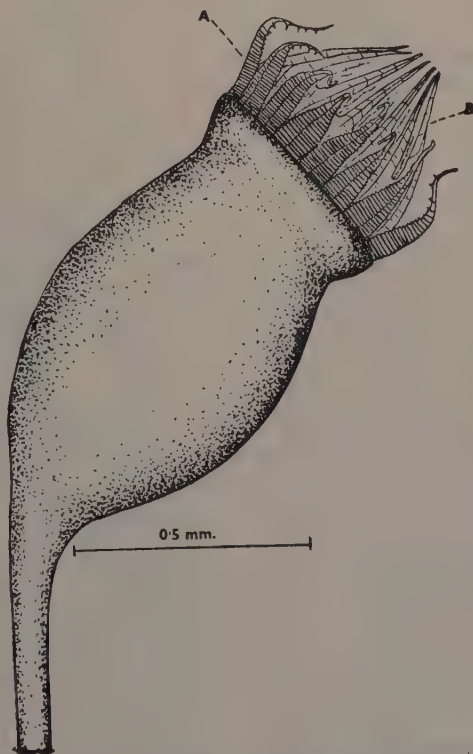


Fig. 4. *Eurhynchium confertum*.

Mature capsule showing peristome. To simplify the picture the back half of the peristome is not shown. A, outer peristome. B, inner peristome.

closely packed transverse plates about $0.5\ \mu$ thick and much the same distance apart, with the plane of each plate at right angles to the length of the tooth (Fig. 8). What occupies the narrow slits between neighbouring plates is not clear. It may just be air. If this is so the actual exposed surface for water absorption from a damp atmosphere is enormous and this may partly explain the rapidity with which the tooth responds to changes in humidity.

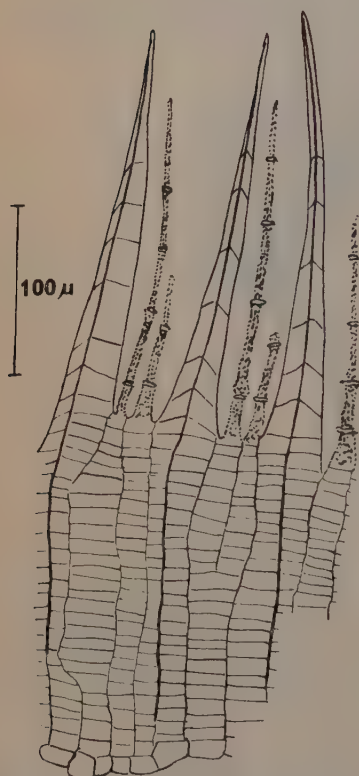


Fig. 5. *Eurhynchium confertum*.
Part of inner peristome (viewed from outside) showing three inner teeth and the cilia between.

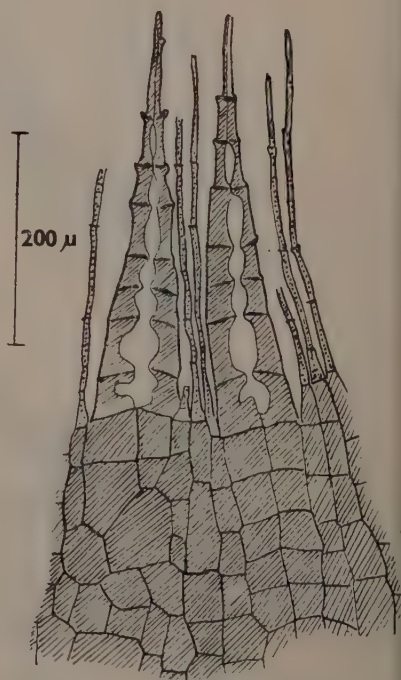


Fig. 6. *Mnium hornum*.
Part of the inner peristome (looking at the inner surface) showing two teeth and a number of cilia.

The number of spores in a capsule of *Eurhynchium confertum* has been determined approximately using a haemocytometer technique. The estimates for four separate capsules were 280,000, 480,000, 500,000 and 700,000.

A capsule from which the lid had recently separated was laid on its side on a glass slide. It was breathed on gently and then allowed to dry. As a result, some spores were discharged to a distance of several millimetres. The capsule was then gently moved to another part of the slide and the procedure repeated. This was done again and again, and on each occasion the number of discharged spores was counted. The procedure was repeated 171 times and a total of 15,647 spores was discharged. Thus, on the average, at each backwards movement of the outer teeth 91 spores were liberated. Initially, the numbers were rather higher and then tended to fall off. It is clear, thus, that drastic and rapid changes in humidity may lead to the discharge of large numbers of spores. However, it seems unlikely in *Eurhynchium*, where the peristome faces upwards with the axis of the capsule at an angle of about 60° from the vertical, that movement of the outer teeth can be responsible for the discharge of a large proportion of the spores. Fig. 3 shows a section through a mature dehiscent capsule and, on examining this, it is difficult to see how more than 5 or 10% of the spores could be scooped out by the teeth. However, such a percentage might amount to tens of thousands of spores.

In *Mnium hornum*, where the capsule is nearly pendulous, it is possible that movements of the peristome teeth might, perhaps, be more concerned with discharge, since as spores, initially present within reach of the outer teeth, are liberated, more may move down under the influence of gravity and thus replenish the supply available to the teeth. In this connection a vital point is whether the spores are dry or sticky. It has been stated that they are sticky (Goebel, 1895) but this is not so. The wall in the dry mature capsule of *Mnium hornum* is translucent and the spore-mass can easily be seen within (Fig. 9). If a mature capsule with the lid still intact is examined it will be observed that the upper surface of the spore mass, which about half fills the capsule, is more or less horizontal. Further if the capsule is inverted the spores all drop down to the bottom. Indeed, the spores behave just like sand in an hour-glass. Thus as spores are liberated from

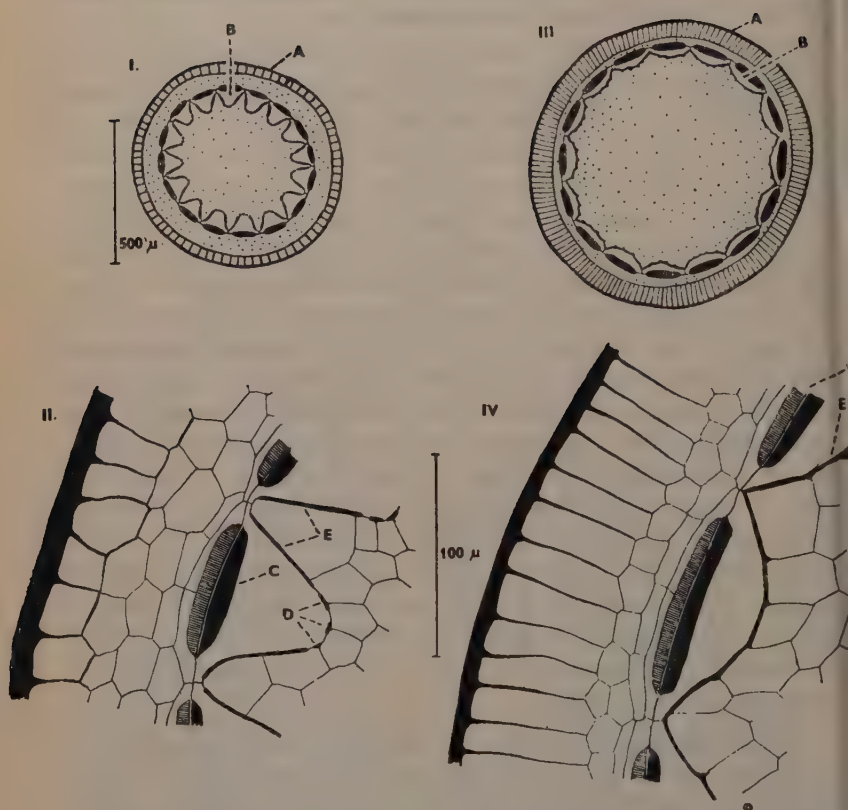


Fig. 7. *Mnium hornum*.

I, transverse section of full-grown green capsule cut in the operculum region half way between the diaphragm and the tip. Cells of the operculum (A) and of the peristome (B) are shown, but the remaining thin-walled tissues are indicated by stippling. II, a small part of I giving high power details; C, outer peristome tooth; D, three cilia; E, inner peristome tooth. III, transverse section similar to I but near the diaphragm: A, cells of operculum, and B, cells of peristome. IV, high power details of part of III: C, outer peristome tooth; E, inner peristome not dissected at this level.

the peristome region more may be expected to fall down and take their place. However, this does not mean that the peristome teeth are concerned to a great extent in spore liberation. When conditions are dry and the outer teeth are reflexed, the powdery spores sift out through the inner peristome with the greatest of ease every time the wiry seta vibrates in a gentle breeze. Indeed, there is no reason to believe in *Mnium* any more than in *Eurhynchium* that violent discharge by the outer peristome teeth is of significant biological importance.

With such an elaborate mechanism as the moss peristome it is almost inconceivable that it is mere decoration of use to the taxonomist but without significant biological importance. However, it is only by careful experiment and by observation in the field that the significance of the peristome can be evaluated. Most students of mosses would probably agree that fundamentally the

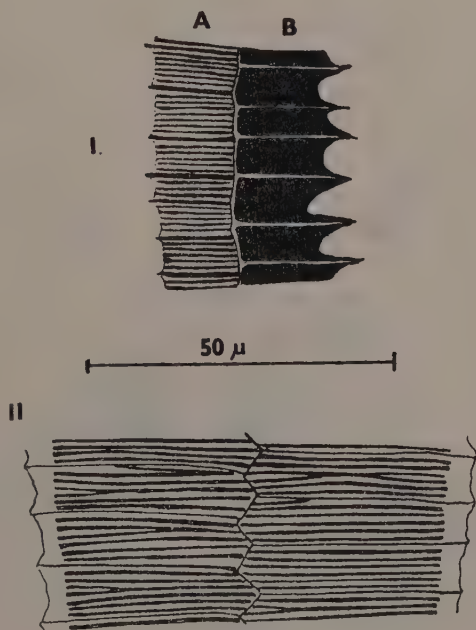


Fig. 8. *Eurhynchium confertum*.

I, part of an outer peristome tooth as seen in longitudinal section of the tooth. A, outer layer showing plates of thickening; B, inner layer. II, view of the outer surface of part of a tooth showing plates of thickening.

importance of mobile peristome teeth is the closure of the capsule under damp conditions and opening under dry. Violent discharge when it occurs may be regarded merely as an accidental concomitant of the opening mechanism.

If this interpretation of the survival value of the complex peristome is correct, there is the further question of what is the advantage of spores being liberated under dry as distinct from damp conditions. Indeed aerial dispersal in damp air would seem to be more desirable than dispersal in dry air for spores would probably survive longer under damp conditions than under dry. The solution of this problem is probably connected with the other meteorological conditions associated with dampness and dryness, in particular wind and the general turbulence of the air. Dr. P. H. Gregory has rendered a great service to the study of spore dispersal by his insistence that the problem of aerial dispersal is essentially a meteorological one and that an initial problem for the plant is the liberation of spores into turbulent air (Gregory, 1945 and 1952). In immediate contact with the ground is a layer of non-turbulent air in which flow is laminar. Spores liberated into this layer soon sink under their own weight to the ground.

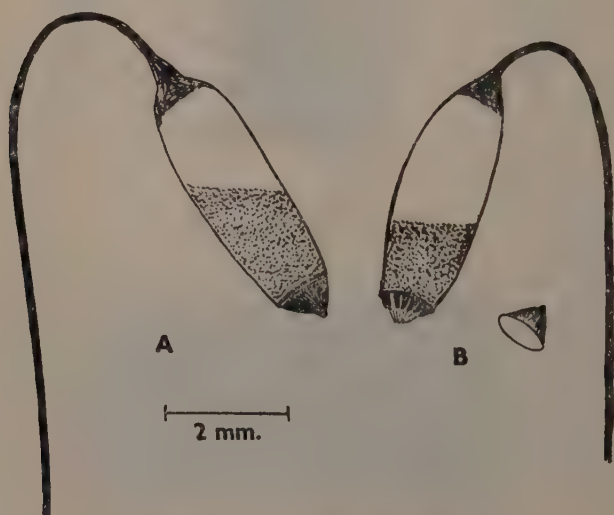


Fig. 9. *Mnium hornum*.

A, ripe capsule—the operculum, seta and extreme base of the capsule are opaque but the spores, shown dotted, can be seen through the semi-transparent capsule wall. B, another capsule with the lid removed.

Above this is a layer of turbulent air—a layer of eddies. Once in this turbulent air the tendency for the spore to sink is of little significance. Its fate is determined by the behaviour of the air-mass in which it has become incorporated just like a water droplet in a mist or cloud. The thickness of the non-turbulent layer varies with general meteorological conditions. It may only be a few millimetres or even a few microns deep, but when conditions become very still, as often just after sunset, the depth of the laminar layer may be reckoned in metres. Teleologically speaking it might be said that the whole point of the erect seta in a moss is to raise the capsule above the ground level so that it is at least sometimes in the turbulent layer of air. In passing it might be remarked that from the point of view of dispersal the longer the seta the better, but the possible height is limited by the absence of a vascular system. In other archegoniate plants, where a vascular system exists, spore liberating mechanisms are exposed much higher above ground level as in the fertile frond of *Blechnum spicant*, the spike of *Ophioglossum vulgatum*, the strobilus of *Lycopodium clavatum* or the cone of *Equisetum arvense*. There do not appear to be any readily available data, but it seems very likely that there is a close correlation between humidity at capsule level and lack of turbulence at that height.

The whole problem of spore liberation and dispersal in mosses now needs experimental study both in the laboratory and in the field. In the field, variations in the spore-content of the air above a patch of capsule-bearing moss could be studied with a Hirst trap (Hirst, 1952), at the same time following, by suitable micro instruments, the humidity and air movement at capsule level. The effect of rain drops striking the capsules should also be investigated. In the laboratory there is much to be learned by studying spore liberation from capsules in a wind tunnel. There are a number of obvious questions to be asked. Under controlled conditions of turbulence how is spore liberation affected by the humidity of the air? Are repeated and violent changes in humidity of any real significance in spore liberation? How far does vibration of the wiry seta play a part in spore liberation?

One final possibility is worth mentioning. Brodie and Gregory (1952) have shown that in the vase-like podetium of the lichen *Cladonia pyxidata* wind blowing across the mouth produces vortices which may suck out the powdery soredia from the vase.

Perhaps also characteristic vortices may develop associated with the peculiar form of the peristome and these may have some significance in spore liberation.

Our knowledge of spore liberation in mosses has in the past been based on a contemplation of structure, but it is always unsafe to deduce function from form and the time is now ripe for quantitative experimental work on this problem.

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SOME ASPECTS OF MICROSPORE MORPHOLOGY.

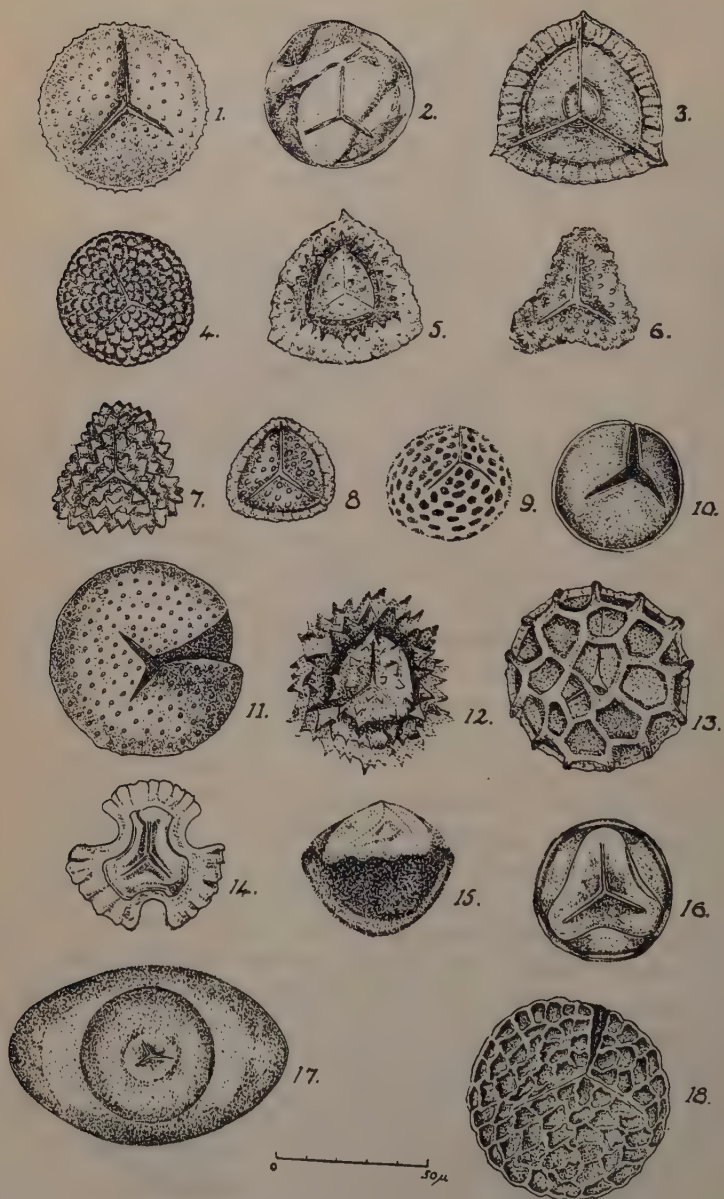
By ELIZABETH M. KNOX
(Heriot-Watt College, Edinburgh).

Palaeobotanical investigations until recently have been mainly concerned with macrofossils, but within the last thirty years microfossils, notably spores and pollen grains, have assumed increasing importance both from the botanical and the geological point of view, since they are of some value in palaeo-ecological and phylogenetic studies and they are of considerable significance in the elucidation of problems of stratigraphy.

The object of the present paper is to indicate what may be the main trends in microspore morphology from the earliest appearance of spores and throughout the Palaeozoic era, and to refer also to existing plant phyla whose spores exhibit similar morphological characters to those in early geological times.

Probably the oldest known structurally preserved plants are those described by Tyler and Barghoorn (1954) from the Pre-Cambrian rocks of Ontario; they report remains including algae with cyanophycean affinities and two forms of fungus mycelium. Carbon remains of algae have also been described by Fenton (1946) from Pre-Cambrian rocks of Canada. Microspores have been reported from rocks of Cambrian age in India and Europe, but the material may require further investigation, coming as it does from areas of uncertain stratigraphic sequence. Certain of these microfossils reported as deriving from vascular plants of Cambrian age are now known to have been mis-interpreted.

The earliest undoubted vascular plants have been described from the *Monograptus*-bearing Silurian beds of Australia by Lang and Cookson (1935). One of these plants, *Baragwanathia longifolia* bears sporangia containing slightly oval smooth spores of approximately $50\ \mu$, and another, *Zosterophyllum*, has smooth, round spores ranging from $45\ \mu$ to $75\ \mu$ in diameter; the latter plant with its spores is recorded also from the Lower Devonian in Scotland, Germany and the United States of America. From the Old Red Sandstone of Wales, Croft and Lang (1942) describe the papillate spores referred to as *Sporogonites exuberans*, whereas from the Downtonian beds of the same age in Spitzbergen, Høeg (1942) figures a variety of spores with smooth,



granular or papillate exines, as well as others with short conical protuberances or with spines of varying length, while in one form the spines terminate in grapnel-like processes.

From the Middle Old Red Sandstone of Scotland, Lang (1925) illustrates nine spore types showing increasing complexity in sculpturing from smooth, to finely granular and papillate, as well as a spinose type similar to one described by Høeg from the Spitzbergen material. Two further varieties are figured possessing wing-like flanges, but all these spores are of unknown parentage. In addition to these trilete spores, Lang describes resting spores of two fungi having thick walls, and varying in size from 100 μ -240 μ in diameter.

During the last thirty-five years, knowledge of the Devonian flora has greatly increased especially in the northern hemisphere, and one of the most striking features which has been revealed is the difference which appears to exist among the floras of the three main divisions of the system. In the Lower Devonian so far as it is known, the vegetation was formed of low-growing slender plants, herbaceous or semi-aquatic and mostly of simple psilophyte-like forms. During the Middle Devonian, plants attained a higher level of differentiation including representatives of the Pteridophyta, though these were small-leaved, simple plants. The Upper Devonian flora, in contrast, was rich and varied and by this time some plants had developed the tree habit, with large fronds and leaves. The pteridophytes are well represented by a number of genera and a few gymnosperms have been recorded from the rocks of this age. This increasing diversity

Fig. 1-18.

Microspore genera. All $\times$ 500. 1. *Apiculatisporites* (Ibrahim 1933) P. & K. 1954. 2. *Calamospora* Schopf, Wilson & Bentall 1944. 3. *Cirratriradites* Wilson & Coe 1940. 4. *Cyclogranisporites* P. & K. 1954. 5. *Densosporites* (Berry 1937) P. & K. 1954. 6. *Granulatisporites* (Ibrahim 1933) P. & K. 1954. 7. *Lophotriletes* (Naumova 1937) P. & K. 1954. 8. *Lycospora* (S.W. & B. 1940) P. & K. 1954. 9. *Microreticulatisporites* (Knox 1950) P. & K. 1954. 10. *Punctatisporites* (Ibrahim 1933) P. & K. 1954. 11. *Planisporites* (Knox 1950) P. & K. 1954. 12. *Uristatisporites* P. & K. 1954. 13. *Reticulatisporites* (Ibrahim 1933) P. & K. 1954. 14. *Tripartites* (Naumova 1937) P. & K. 1954. 15. *Tholisporites* Butterworth & Williams 1958. 16. *Rotasporea* Schemel 1950. 17. *Schulzosporea* Kosanke 1950. 18. *Convolutispora* Hoffmeister, Staplin & Malloy 1955.

is directly reflected in the larger number of spore types and in their variety and the complexity of their morphology. Naumova (1953) figures spores from the Upper Devonian of the U.S.S.R. which possess a thick "perispore" and she regards this feature as one which is characteristic of spores of this period. From the Upper Devonian of Western Canada thirteen spore genera are reported by Hoffmeister *et al.* (1955), all of which have been recognised from rocks of the same age in Europe. These thirteen form genera are:—*Apiculatisporites*, *Calamospora*, *Cirratriadites*, *Cristatisporites*, *Cyclogranisporites*, *Densosporites*, *Granulatisporites*, *Lophotriletes*, *Lycospora*, *Microreticulatisporites*, *Planisporites*, *Punctatisporites* and *Reticulatisporites* (Figs. 1-13).

In a recent examination of samples from a bore-hole in Dumfriesshire, which penetrates down into the Calciferos Sandstone Series of the Lower Carboniferous of Scotland, the microspore content of the coals was found by the author to include representatives of all the thirteen genera noted above as occurring in the Upper Devonian rocks. The results of the investigation are not yet published, but they suggest that these two systems appear to be floristically continuous, a conclusion reached by Jongmans on the basis of his examination of the megaflores of Europe and other parts of the world. Jongmans (1952) states:—"It is a well known fact that there is no sharp separation between the lower part of the Mississippian and the upper part of the Devonian. Botanically, it might even be more reasonable to unite by a transition series the Upper Devonian with the lower part of the Mississippian. This transition contains a flora which I name the *Lepidodendropsis-Cyclostigma-Triphylopteris* flora. Floras of this type are known all over the world—Peru, United States, Europe, Egypt, China, etc., and show a remarkable uniformity."

In a recent paper on the *Small Spore floras of coals of the Limestone Coal Group and Upper Limestone Group of the Lower Carboniferous of Scotland*, Butterworth and Williams (1958) figure over 100 microspore species from 33 genera. This varied microflora is in contrast to the 37 species found by the author from the Calciferos Sandstone Series near the base of the Lower Carboniferous and it indicates the increasing richness attained by the flora during Carboniferous times.

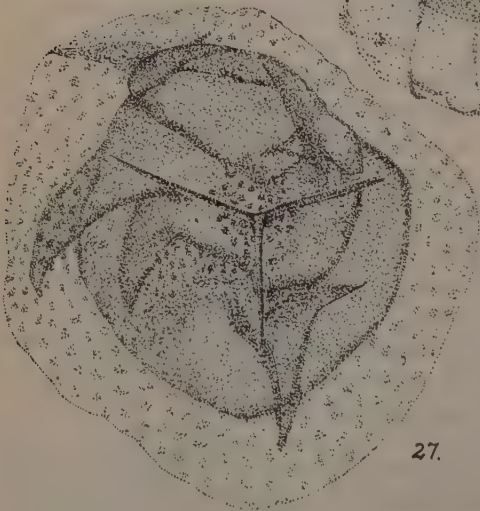
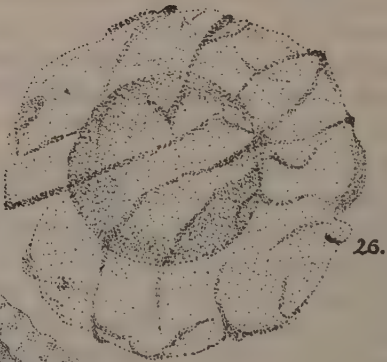
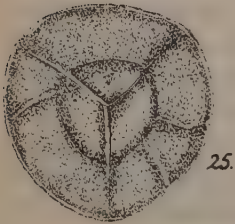
Two genera, *Lycospora* and *Densosporites* (Figs. 8 and 5) are prominent in the spore assemblages of the Limestone Coal Group, both being represented by several species. These two genera have been recorded from the Devonian and their constituent species become a conspicuous component of the microflora in the Coal Measures of the Upper Carboniferous. Five other genera are also characteristic of the Limestone Coal Group, namely:—*Rotaspora*, *Tripartites*, *Tholisporites*, *Convolutisporites* and *Schulzospora* (Figs. 14-18) of which only the last two named persist into the lower part of the Upper Carboniferous.

All the genera represented in Devonian strata have been recorded throughout the Carboniferous period and some additional genera which are infrequent in Lower Carboniferous times are of common occurrence in the Upper Carboniferous as for example, *Raistrickia*, *Triquitrites*, *Verrucosisporites* and *Acanthotriletes* (Figs. 19-22). Monolete spores of the genus *Laevigatosporites* (Fig. 23) are a common and characteristic constituent of the microspore assemblages of the Coal Measures and are conspicuously absent from the lower strata.

Other types which increase in frequency during the Palaeozoic era are those with bladders. In the Devonian strata monosaccate spores are recorded, which also persist in the Lower Carboniferous though, with the exception of *Schulzospora*, they make only a minor contribution to the assemblages. The most frequently observed are *Glomospora* and *Remysporites* (Figs. 26 and 27), whereas in the Upper Carboniferous, the genus *Endosporites* (Fig. 25) is a common member of the flora and the spores of *Florinites* (Fig. 24) appear for the first time.

It will be recognised that during the Palaeozoic era great variety in spore morphology was already achieved, spore sculpturing and ornamentation tending to become more elaborate and complex, culminating during Carboniferous times. The Coal Measures epoch was the age of pteridophytes and pteridosperms, after which they decline in importance, while gymnosperms and later angiosperms are in the ascendant.

Our knowledge of the parent plants of the great majority of fossil spores is very imperfect, though it is gradually being augmented by fresh discoveries and the use of new techniques. It is of interest to record some of these microspores of which the



parent plants are known, and to relate them, if possible, to their modern equivalents.

The oldest known spores were simple, round, smooth types and these have been found associated with Devonian Psilophytales, as for example *Rhynia*, *Hornea*, *Asteroxylon*, etc. (Lang, 1925). The smooth, trilete spore form has been repeated many times during the evolution of the Pteridophytes and recorded from fossil Filicales, e.g., *Scoliopteris* (Mamay, 1950), *Discinites* (Remy, 1957) and *Protopitys* (Walton, 1957), and also from Calamarian plants (Hartung, 1933, and Anderson, 1954). At the present day many examples can be cited of similar smooth spores, some spherical as in Equisetales and Mosses; others triangular or sub-triangular can be paralleled in most of the Cryptogams, from the Algae, Selaginellas and several Fern genera.

As has been indicated, spore sculpturing and ornamentation in early Devonian times was mainly in the form of granules or minute tuberculate or spinous projections, and these patterns were added to and elaborated till by the end of the Carboniferous period the variety in spore form and ornamentation was very great indeed. Some conical or spinous outgrowths from the exine were relatively short as seen in the fossil pteridosperm *Alcicornopteris* (Walton, 1949) or the fern *Sphyropteris* (Remy, 1957); others were long and thin as in *Archaeopteris* (Arnold, 1936); or minute and closely set as in *Acitheca* (Remy, 1957) and the pteridosperm *Crossotheca* (Kidston, 1906). Other protuberances were rounded and tuberculate, either small and crowded as in *Zygopteris* (Remy, 1957) or large warts, widely spaced or irregular as in *Psaliangium* (Remy, 1957). In *Botryopteris* (Mamay, 1950) a peculiar form of straight-sided stick-like projection is seen. A regular reticulate pattern becomes common as well as various arrangements of broken ridges and channels such as occur in

Fig. 19-27.

Microspore genera. All $\times 500$. 19. *Raistrickia* (S.W. & B. 1944) P. & K. 1954. 20. *Triquitrites* (Wilson & Coe 1940) P. & K. 1954. 21. *Verrucosiporites* (Ibrahim 1933) P. & K. 1954. 22. *Acanthotriletes* (Naumova 1937) P. & K. 1954. 23. *Laevigatosporites* Ibrahim 1933. 24. *Florinites* S.W. & B. 1944. 25. *Endosporites* Wilson & Coe 1940. 26. *Glomospora* Butterworth & Williams 1958. 27. *Remysporites* B. & W. 1958.

Waldenburgia (Remy, 1957), *Scoliopteris* (Mamay, 1950) and *Senftenbergia* (Radforth, 1939). Microspores similarly furnished with variously disposed outgrowths can be recognised amongst present day members of the Bryophytes, Lycopods, Selaginellas and Ferns (Knox, 1938, 1939, 1950).

A common constituent of the Carboniferous spore assemblages is the spore genus *Lycospora* (Fig. 8). These spores have a narrow equatorial flange and are known to be of Lycopsidean origin. Spores of this type have been found associated with *Lepidostrobus* (Kidston, 1923; Chaloner, 1953a). Another commonly occurring Carboniferous form is the annulate *Densosporites* (Fig. 5) which can be compared with *Selaginella scandens* or with *Lophosoria quadripinnata* (Knox, 1938, 1950) to which the fossil genus bears a striking resemblance.

Less common in the Palaeozoic but nevertheless important stratigraphically are the spore types with encircling bladders. To this group several genera belong, notably *Schulzospora* (Fig. 17) and spores of this form have been isolated from fructifications of the fossil fern *Simpliotheca silesiaca* (Remy, 1955). Other monosaccate types are *Remysporites* and *Endosporites*. *Remysporites* is a recently created genus (Butterworth and Williams, 1958) of large spores with finely reticulate bladders which has been named after Remy, who described similar spores from the pteridosperm *Paracalathiops* (Remy, 1954). The spore *Endosporites zonalis* (Fig. 25), a characteristic zone fossil of the Coal Measures, has been described by Chaloner (1953b) from *Lepidostrobus zea* and it has a close counterpart in the modern *Selaginella wallacei* (Knox, 1950).

The earliest known occurrence of a typically bi-saccate spore is from the Coal Measures in England and described by Williams (1955) under the name *Pitysporites westphalensis* as an Abietineous type of pollen grain.

Monolete spores make their first undoubted appearance in the Upper Carboniferous as a conspicuous element of the microflora. In the Coal Measures smooth bean-shaped spores of various sizes are common (Fig. 23) and are generally regarded as Filicean in affinity, though similar spores are known from the fossil Articulatae as for example *Bowmanites* (Andrews and Mamay, 1951).

Spores similar to some of the fossils with more unusual sculpturing can be paralleled among the modern ferns as for example, *Rotaspora* which is not unlike the present day *Hicriopteris laevissima* (Erdtman, 1957) and *Triquitrites* which is akin to *Cheiropleuria bicuspis* (Erdtman, 1957); there are still fossil genera of which no modern equivalents are known.

SUMMARY.

Amongst the earliest land plants of Silurian and early Devonian times microspores were mostly spherical and simple in sculpturing. With increasing mastery of a land environment great variety in the pattern and ornamentation of spores was achieved, reaching a climax in the Coal Measures when Pteridophytes and Pteridosperms were dominant constituents of the flora. At this period also Gymnosperms were becoming more numerous and constituted an important element in the vegetation. Of the very large number of micro-fossils which have been described, the majority of the genera can be paralleled at the present day from Bryophytes and Pteridophytes. Of the Angiosperms, however, no pollen has as yet been recorded with certainty from rocks of Palaeozoic age.

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SOME FUNDAMENTAL CONSIDERATIONS ON THE
"NEW MORPHOLOGY".

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Schüler: Doch ein Begriff muss bei dem Worte sein.

Mephistopheles (of all people):

Schon gut !

Mit Worten lässt sich trefflich streiten,

Mit Worten ein System bereiten,

An Worte lässt trefflich glauben, ...

J. W. Goethe, *Faust* I.

In 1932 H. Hamshaw Thomas introduced the term "New Morphology", meaning to indicate that since Paleobotany started to play its part in the interpretation of organs of vascular plants, something fundamental has altered the face of a science so familiar of old and seemingly so well understood. Although a few inveterate morphologists took some offence at the term, which was inoffensive in itself, most investigators interested in the dynamic side of Morphology agreed that paleobotanical evidence more and more affected our insight in morphological problems; it first filled up some awkward gaps, later on joined some loose threads and recently brought about the conviction that some important points in the Morphology of recent Cormophyta, so far either unexplained, or unrecognised, or just neglected, could now be seen in a new light, enabling us to distinguish some lines more clearly both in themselves and in an integrated whole. Speaking for myself, I started to think along these lines more than twenty years ago (Lam, 1936) and when my thoughts in this respect first crystallised (Lam, 1948) it was in no little way due to Professor Matthews' presidential address of 1941.

We are still very far from distinguishing the real face of the "New Morphology", but it seems to me that our present knowledge enables us to distinguish outlines whose significance can no longer be misunderstood and which have only to be investigated more closely to allow us to gaze at a picture of infinitely

more harmonious lines than that which is shown by the present Morphology, which is still mainly a Morphology of Angiosperms;¹ this situation has entailed a most confusing terminology, as we shall see presently. To this situation Goethe's well-known words, used as a motto in the heading of the present paper, are applicable.

Meanwhile, it is not only Paleobotany which initiated this development, though it may have put it on the move. Immediately involved are our concepts of homology and these cannot be cleared up without the help of genetics, a field which in this respect has so far hardly been tackled. Only slightly better is the situation regarding another fundamental branch of botanical science, morphogenesis, which could also be called physiological (or experimental) ontogeny, with its hardly-explored implications (*cf.* Bünning, 1953).

The "classical" Morphology knows of three basic organs only: stem, leaf, and root. Paleobotany and typology have made these merge into the most primitive "vascularised thallus", undifferentiated but for its obvious polarity. This was only natural and it might have been predicted, if only we had thought of it out of an unbiased mind. As soon as time as a dimension is taken into account, everything merges into everything else until the first imaginable living matter is reached, and perhaps beyond.

In the light of this conviction, the wish enters our mind to reverse the chain and to try and reconstruct the divergences.²

¹W. Zimmermann (1952, p. 456, and 1953, p. 73) has misunderstood the term "Angiosperm-centred" (Lam 1948, p. 108) in a rather curious way. He thinks it means "that it (the 'Old Morphology') started from Angiosperm-like 'Urpflanzen' and tried to deduce therefrom the other plants." I of course never thought, let alone wrote this, but used the term only in regard to terminology which, in spite of many new discoveries of primitive land plants, continued to remain the main source for morphological terms.

²The organic system is clearly a diverging one and the recent groups, particularly the older (lower) ones, are more sharply delimited and taxonomically isolated than the younger (higher) ones.

This general phenomenon seems to call for a general explanation which, I think, is also applicable to the origin of life. It may well be that the origin of life as well as that of new levels (taxa of higher order) had the nature of an explosion, in the sense that considerable changes may have been brought about in periods which were very much shorter than those between the "explosions".

On doing so it is soon found that the downward way is far easier to follow than the upward one, because in the former case (so to speak, looking down a telescope from the object-lens), our starting point is the better-known results and in the latter a less differentiated polymorphous group (looking as it were, through a telescope from a very arbitrarily chosen viewpoint from the ocular lens into a wide field of possibilities). It is also comparable to what we experience in our individual life; if, in our old age, we look back to our youth, the line followed seems clear and self-evident (though we are aware that it was by no means the only possible one), but on trying to imagine what may happen in future when we are still young, we find that there is no possibility of predicting our future course, even for to-morrow.

In Paleontology it is one of the well-known and insufficiently explained difficulties that what we would call real intermediates are only very rarely actually found, perhaps because they have been rare, or soon passing, perhaps because we try to insert them with the tenacity of conservatism into some of the groups we are familiar with, but perhaps mainly because of what we expect on account of misinterpretations of more recent forms.

In the meantime, in our attempts to reconstruct, it is again and for obvious reasons easier to follow development of single organs or characters than of taxa. If the first of these courses is taken, we feel that there are only two elementary processes in evolution, although these are mysterious enough, *viz.* growth changes, and differentiation. These two are of course not sharply delimited. Both are likely to be ascribed to genetical factors, and whereas growth changes are to be visualised as more or less gradual phenomena of tissues (meristems), differentiation is probably a more sudden process of cells.

This view, which has also been advocated by geologists (Umbgrove, 1942), need not imply occurrence of "large mutations" on whose bases patterns on a smaller scale were worked out, recalling Cuvier's catastrophes theory in a modern form. Should it have been otherwise, i.e. should life still continue to originate, and should level changes have continued to operate after their start, our present system would surely show a quite different picture. In fact, it should then be expected that the gaps would be much less sharp or even non-existent. It might even be supposed that life itself was a gigantic mutation of matter and that its evolution is pulsating with outbursts of perhaps gradually diminishing force, period, and amplitude.

If we say that a fertile and a sterile telome, e.g. in *Rhynia*, are homologous on account of their position, we may speak of differentiation. Investigating the process at a deeper level, we find that in some cases one or a few cells in sterile telomes undergo a reduction division while the surrounding cells remain diploid vegetative cells.³ It seems obvious, that a previous cell- (or rather nucleus-) division resulted in two different daughter-cells, one with and one without the potency of forming haploid nuclei. Differentiation, therefore, is a process starting with a cell- (nucleus-) division and resulting in two daughter-cells with different potentialities or functions (cf. Bünning, 1953, Prat, 1945).⁴ The difference may relate to the origin of a specialised reproductory cell or to the position of the spindle-axis (see Hendriks, 1955, also Zimmermann, 1952, 457-463, figs.1, 3 and 4) compared to that of the other daughter-cell, resulting in an outwardly-directed cell with a different function inside or outside the tissue (ramification, leaf-formation); and so on and so forth. In all cases of this kind, the homology of the daughter cells is beyond discussion, even though we do not know what really happens physiologically and genetically (mutationally?) whenever such differences in the daughter-cells of one mother-cell appear.

Similarly, in the case of growth changes, homology rests on the comparison of organs to which these changes are ascribed, but it is clear that their examples are more vaguely limited as the differences grow larger. At any event, since meristems ultimately start with a single cell, the two elementary processes of evolution are only gradually different, as seems true for everything in nature.

Returning to practice we may conclude that homology is, to begin with, to be referred to in the following cases: sterile-fertile, and male-female. Now, the question arises, can we safely go any farther? Of course we can, though the term "safely" is only

³Obviously this is to be considered a case of teratology or, teleologically speaking, of atavism. The original differentiation of sterile to fertile clearly lies very deep in the roots of life, probably in the unicellular stage.

⁴Prat (quoted from Newman) delightfully describes this as follows (p. 582): "Le premier grand fait est que la cellule initiale entre en division inégale, l'une de ses filles retenant certaines propriétés . . . tandis que l'autre en manifeste de différentes . . .".

applicable in a subjective way, as has been alluded to above when speaking of growth changes.⁵

Various recent publications (Bünning (1953), Catalano (1956), Fulford (1956), Hendriks (1955), Karstens (1958), Melville (1957), Roth (1957), Zimmermann and Heller (1956)) confirm that the processes of cell-divisions in tissues are so extremely complicated from all possible viewpoints, that for the time being we cannot hope to disentangle them sufficiently to understand *in toto* the homology of tissues or organs, except some whose particulars give comparisons some footing. We have to accept this situation as it is and jump the gulf rather blindly though not without confidence, hoping for a firmer basis in a future we are too impatient to wait for in the face of so many urgent problems which demand a solution, even if admittedly imperfect or more or less biased.

Before continuing the above issue, let us—keeping within the phylum Cormophyta—recall again the old morphology and look at the concept “leaf”.⁶ At first sight there seems to be no difficulty; a leaf, or, to use a wider term, a phyllome or phylloid, is a lateral organ (lateral to the stem, that is), having, or allegedly having had, a special function. In the Phanerogams there is the additional feature that a leaf, however shaped, is recognisable by its axillary bud. However, on closer investigation, even within the Angiosperms, there are some weak spots in this reasoning. I need not here dwell upon cases like that of the so-called “terminal” leaf, or the leaf-like shoot, nor upon the question how to distinguish between leaves and enations, but it may be useful to recall the fact, that there is no common opinion on the identity of such floral organs as stamens, carpels and, to take one more step, the integuments of the ovules.

In the vegetative sphere also things may not always be what they look like. The anatomical limit between monofacial and bifacial organs which should enable us to distinguish between axes and leaves, respectively, is by no means sharp and sometimes definitely not convincing. Even the axillary relationship between

⁵Zimmermann (1953, 71-75) gives a short historical survey of the concept of homology but retaining the traditional definition of “organs of identical origin whether or not, in the course of phylogeny, changed in shape, position, and (ontological) time of appearance”, he does not tackle the core of the problem.

⁶*Cf.* Zimmermann (1953, 73).

leaf and axis may lose something of its argumentative power on considering the existence of serial buds; and one wonders what the said relationship actually represents.

The uncertainty increases as we climb down the phylogenetic ladder. In Gymnosperms, perhaps with the exception of the Cycadopsida, we may be fairly sure of the axillary relationship of phyllotaxis and stachyotaxis. But there are some nasty exceptions, again in the reproductory area. The microsporophylls of the Conifers, for instance, while generally interpreted as phyllomes, so far as I know never show the slightest trace of an axillary bud, except in some bisexual cones (*cf.* Nozeran (1955), p. 40, fig. 44), and the same probably holds for the sporophylls of both sexes in Cycads. I shall return to this point later.

"Carpels", traditionally phyllomes, have been recognised only with the greatest difficulty or construed in a very forced way in such plants as *Ginkgo* and Cycadeoidea, not to speak of many others in which they were simply reasoned away by invoking the process of reduction, a notion which, I think, is in several cases of a very doubtful value, when critically judged.⁷

Digging deeper into the system, though without any pretence of striving for completeness, we may look at the ferns. There is no clear relationship here between "leaves" and ramification, and moreover there are cases such as that of *Lygodium* in which it is impossible to give a sensible definition of what in this plant should be called a "leaf". A similar reasoning is applicable to e.g. *Tmesipteris* which also seems to possess a truly terminal leaf.

The difficulties accumulate on digging farther: are fern-ramenta some sort of leaves or parts thereof, or just enations? What about indusia, sporocarps, one-nerved leaves of Sphenopsids, Lycopside, Moss-gametangiophores, the nerveless leaves of *Asteroxylon*, the warts and prickles of *Rhynia*, *Psilophyton*, *Drepanophycus*, the leaf-like structures of *Delesseria* and

⁷The term reduction may, in my opinion, mean at least two things:

(1) a process of loss of differentiation in the sense of Lamarck, often initiated by a loss of function, *i.e.* a sort of negative growth change; and (2) retention in a part of a population of a primitive character-phase, whereas the same character may have evolved in other parts of the original population. Particularly when the original population disappears, controversial opinions are possible as to whether the simple type which survived, is to be considered "primitive" or reduced from a more advanced one.

Caulerpa? Where does homology end and analogy start? The answers are necessarily subjective and the conclusion is that "leaf" is worthless as a morphological concept; it is rather at best a functional notion.

Let us now retake the thread of our interrupted reasoning above. Are there any organs which promise a more or less continuous line in which we can recognise homologies with reasonable confidence? Taking for granted that the telome theory is at least a concept worth being given a fair trial, we must state that the telome is to be our fundamental organ of issue. Leaving apart all considerations concerning the problem of the "enation leaf", two features are evident: the ramification is fundamentally dichotomous, and a telome is recognised as such by the possession of a stele.

Before going any further along this line, it must be stated that lateral branching, as opposed to dichotomy of the growth point, has been mentioned as another possibility by many authors, and it must be admitted that we know nothing about which groups of higher Thallophytes contrived to conquer the land. It is quite possible that some of them had developed the lateral mode of branching, but in this respect I think the following points should be considered: 1. It is conceivable that ramified Thallophyta arose from coenobia with growing cells in several directions and that this may have been the origin of lateral growth points next to apical ones (*cf.* Zimmermann and Heller, 1956).

2. In view of the polarity, however, which must have been acquired as soon as plants grew attached to a fixed substratum, it is more probable, particularly in land plants, that the very apex retained its growing potencies rather than that these potencies were kept back in a latent state in adult parts of the thallus.

3. Whatever mode or modes may have been inherited by the earliest land plants, a very heterogeneous group indeed, on account of what we know of younger groups, it seems fairly certain that apical dichotomy was the first successful and most general way of ramification, which only later on, as differentiation increased, was gradually replaced by other types through overtopping processes. Accordingly we will, in the following con-

siderations, start from the viewpoint of dichotomy as the most fundamental mode of ramification in land plants.

In comparing more highly developed groups, the picture is, in the vegetative sphere, soon blurred, *e.g.*, by overtopping, coalescence, planation, webbing, and suchlike processes, and its details are only recognised with difficulty so that interpretations become more and more uncertain. This is both the case in the microphyllous groups, in which one-nerved leaves are usually considered the result of reduction of a syntelome, and in macrophyllous ones in which the exuberant branching of telomes has led to complicated patterns of nervation. In all these cases, however, nerves are to be considered homologous to protostelic "stems" with a special function. Open nerve endings in macrophyllous plants may represent true telomes, solitary nerves in microphyllous ones are probably mesomes, of which the telomes have been "rubbed off" by reduction. As has been shown by Van der Hammen (1948), open nervation occurs as far up in the system as the Angiosperms and it is proportionally more frequent lower down in the system. To my mind there is not the slightest doubt that all nerve ramifications are homologous with the original dichotomy in *Rhynia* (and in Thallophytes), which later on maintained itself in so many organs of a higher level like stems and roots, *e.g.*, in the Lycopsidea and even in some Angiosperms (palms? see Bremekamp, 1956, p. 133). In fact, dichotomy is actually universal, though it is often hidden by younger processes, as I will show later on. It is still to be seen, in an overtopped form, of course, in dicotyledonous root-ramifications.

In this sense, nerves may help us to recognise homologies. This implies that nerveless organs are handicapped, unless obviously related ones are provided with a vascular supply. This is the case, for instance, in the ligules of *Selaginella* which are devoid of any traces of tracheids (Vink, 1953), but whose carboniferous relatives had ligules with a vascular bundle leading to them. Since intermediate forms between *Lepidodendron* and *Selaginella* are unknown, however, we cannot be fully sure that their ligules are really homologous and this is one of the reasons why the problem of the "lyco-leaf" arose in literature, and why its nature as a reduced syntelome (though not entirely without support) could be doubted and the alternative of the enation-leaf got a new impetus.

The lack of a nerve in fern ramenta equally makes it impossible to interpret them as either enation-leaves or reduced telome-leaves and for this reason this organ has to be classed with the lamentable category of enations or epidermal excrescences.

A similar case is that of the indusia and of "the" integuments, which have recently been discussed in a very lucid paper by Ingrid Roth (1957). It seems worth while, in this context, to enter somewhat more circumstantially into this subject, about which numerous authors have expressed themselves in the last century or so. Regarding this renowned problem the literature is rather hazy and though it has recently been cleared up in some respects, it has never been looked upon, I think, in its full phylogenetical significance.

From her study of the ontological development of the integuments of *Capsella*, Roth concluded that "die Integumente, deren Spitzenwachstum von zweischneidigen Scheitelzellen besorgt wird, in entwicklungs-geschichtlicher Hinsicht ebensogut mit Blättern wie mit Indusien homologisiert werden können. Weitere wesentliche Aufschlüsse über ihre morphologische Natur und Herkunft kann uns die Betrachtung der Entwicklungsgeschichte in diesem Falle leider nicht liefern. Eine eingehende Untersuchung der jüngsten Entwicklungsstadien der Samenanlage würde uns hierüber aber vielleicht schon mehr verraten können".

I think that this fair and non-committal statement is about the best which can be expected from one who has intensively and accurately studied ontology, realising with rare impartiality that ontogeny need not be conclusive in the interpretation of phylogenetic speculations. I may add here as my opinion that neither ontogeny nor anatomy can ever have the last word in this field: decisive conclusions can only be yielded by fossil evidence and by a phylogenetical consideration concerning all fields of science involved, including anatomy, histology and ontogeny.⁸

⁸To this is opposed Grégoire's (1931, p. 1301) emphatical statement that "les renseignements fournis par l'ontogenèse (sont) les seuls qui touchent le fond du problème" (of the origin of the carpel), as well as his statement (Grégoire, 1938, p. 297) that all attempts to interpret the morphology of recent plants on the basis of fossil evidence must be "parfaitement vaines".

In this context Kozo-Poljanski, discussing the antagonistic views of H.H. Thomas and McLean Thompson, speaks of "a duel not only between palaeontology and ontogeny . . . (but) a case of a conflict of two different modes of scientific thought."

Nevertheless Roth, in her discussions, gives a well-pondered survey of what has been thought about the origin of integuments in a phylogenetical sense and here, too, she is admirably unbiased, though it is evident that she never let her mind be imbued by the phylogenetical trend of thinking. Accordingly she speaks of "morphologische Deutung der Integumente" in a comparative-anatomical and typological rather than phylogenetical sense.

One of the interpretations of the integument(s) is that they should represent "leaves". This pronouncement stands or falls with the definition of the term "leaf", and in by far the most—if not all—cases concerned this is left to the reader to decide upon; a most unsatisfactory situation, because the term leaf generally suggests a sort of ideal structure, a phyllome, which evokes the picture of an average green Angiosperm leaf.

What is actually meant, however, is a sterile structure, in contradistinction to a fertile one. It may have struck many plant morphologists as peculiar when Hagerup (1934) arrived at the conclusion that the integument of e.g. the Pinaceae is to be considered a megasporophyll; and after having rejected the idea (or rather the interpretative term), I returned to it later on and could even appreciate it although I still have some objection to the term "sporophyll" in this context.

I believe we have to start all over again and, following the course of time, to try and fit in chronologically—or typologically—consecutive forms in an evolutionary logical system.

Again, we start from the terminal sporangia of the Psilophyta, without bothering about from what thallophytic type they may have originated. First there was only one type of sporangium and even here there arose structures which can best be explained as protective. The most primitive of these shows the sporangium in an axillary position. Now what exactly does this mean?

I must confess that it has taken me several years to find the most likely explanation.⁹ Starting from an arrangement in the reproductory region in which fertile and sterile telomes showed their homology by their position, we find developments in two more or less opposite directions: one in which isotomy (or slight anisotomy) is for long preserved, and one in which overtopping became the general principle.

⁹The one given in my paper of 1951, p. 391, fig. 3A is obviously incorrect.

The first of these cases led to the situation found in such phyllosporous plants as the ferns with their mixed syntelomes; the second gave rise to stachyosporous plants in which the sporangia long remained independent and only secondarily were associated with sterile structures. These I have termed stegophylls so as to distinguish them from sporophylls in which sporangia of old formed part of a mixed structure in which they soon were greatly outnumbered by sterile telomes.

In the stachyosporous type (Lam, 1950, p. 520) the original situation was apparently that sterile and fertile (syn)telomes were arranged in one and the same helix, a condition later preserved in the strobili of the Cordaitales of both sexes and in the female ones of the oldest Conifers. When, however, the strobili were still terminal (as was and still is the case in the Lycopsidea) the first and only possible protection of the sporangia was a closer association with sterile organs and I have come to think that the only reasonably imaginable process according to which this may have been brought about is that very early in phylogeny paired organs were formed in which one part was sterile and the other fertile. Such a paired organ should primarily be considered a fertile-sterile dichotomy—originally an isotomous one—establishing itself as a sort of higher unit. A most illustrative example of this is presented by *Drepanophycus* in which the principle still seems to be unfixed and variable (Lam, 1951, p. 391, fig. 3B); the ultimate condition is found in the Lycopsidea, both fossil and recent ones and, *mutatis mutandis*, in Sphenopsida. For obvious reasons, the isotomy was soon replaced by a slight anisotomy in so far as the fertile half got shorter-stalked and the sterile one more or less developed so that it provided a better protection.

In the last-named group (the Sphenopsida) with its enormous diversity, particularly in the Carboniferous, Hirmer (1933) recognised this principle, but on basing on it his "Spaltungstheorie", stating that the fertile half could as well be situated above as below the sterile one, he unfortunately called the whole structure a "leaf", and this has probably been the main reason why the concept, however sound in itself, attracted little attention.

In these protective fertile-sterile units, which I here propose to call *Mixed Protective Bifurcation Units* (M.P.B. Units) the two halves were serially placed, i.e. parallel to the axis. This is only logical, since a collateral arrangement would have had no

advantage from the standpoint of—selectively valuable—protection. Collateral buds are by no means rare, notably in the Angiosperms.

It is also comprehensible that the arrangement in which the upper half of the pair is fertile enjoyed the best protection and therefore the best chance of survival, on account of the fact that sterile parts—the stegophylls—have a geotropical tendency to grow upwards. Yet some highly interesting cases are known, in which the sporangium was situated underneath its sterile counterpart (*Metacalamostachys*, *Cingularia*, *Kallostachys*, the last with fully adnate sporangia), and in these cases, which had, indeed, the best chance to arise in a prolific class like the Sphenopsida, the protection gained was obviously originally less perfect and had to be improved by some additional corrections.

Whereas in the Lycopsidea these M.P.B. Units are mostly simple, consisting only of one (superior) sporangium (a single fertile telome) and one (inferior) stegophyll (a telome or more probably a reduced syntelome), in the Sphenopsida the parts are often more compound, issuing from paired sporangia and repeatedly dichotomised stegophylls, of which the latter soon were reduced to one-nerved leaves or were even, in the strobilus, entirely suppressed (*Equisetum*). It might be intimated that the less close connation of sterile and fertile parts of the M.P.B. Units in the Sphenopsida was one of the reasons why that group disappeared earlier (and in spite of their strong differentiation in the Carboniferous, only survived in some 30 species of one genus), than the Lycopsidea in which the said connation very early provided for a better protection.

Bremekamp (1956, p. 127) alludes to these M.P.B. Units as “this curious arrangement” but his favourite explanation roots in the Old Morphology concept of “splitting”. This often loosely-used notion of which every morphologist seems to have a vague inkling but no one a clear idea, cannot mean anything else, phylogenetically speaking, but the dichotomy with sterile-fertile differentiation mentioned above. It regularly turns up in morphological literature, a good example being the recent study of the floral morphology of Rhamnaceae by Bennek (1958) who interprets—on purely ontogenetical grounds—the small petals and their epipetalous stamens as a “Phyllom-Einheit”, in which serial splitting is considered the original process. Those who are

familiar with my views will understand that my interpretation in cases like these is the old M.P.B. Unit which in the Angiosperm flowers is found in what I consider the stachyosporous type, in which axial (axile, of axis nature) stamens (and ovules or axial placentae) are axillary to phyllomes.

Where in these groups heterospory developed, the megasporangia, as the more vitally important organs, soon obtained an additional protection, a widespread phenomenon in both the vegetable and animal kingdoms. At least this is so in the Lycopsidea in which the sporangia in a very early stage closely grew together with the stegophyll in the female sex, which later on in ontogeny enveloped the fertilised gametophyte and ultimately the "seed". The Sphenopsids are considerably less advanced in this respect. On a higher level the same principle is manifesting itself in what Zimmermann (1956) called the "Schuppenkomplex" of the female coniferous cone,¹⁰ as well as in the stachyosporous Angiosperms (*cf.* the case of the Rhamnaceae, quoted above). In both the two components of the unit are of course polytelomatic. The fact that in the strobili of both sexes in the Cycadales and of the male sex in the Coniferales the sporophylls, though admittedly leaves, are not known ever to produce an axillary bud, whereas in the female coniferous cone the M.P.B. Unit is, at least in principle, always found, can be explained by assuming that in the cases just mentioned, the lower (abaxial) part of the bifurcation (primarily a "leaf") is fertile and that an upper fertile one (primarily an "axis") was suppressed by inhibitory processes. It is a generally acknowledged fact that sterile and fertile are somehow physiologically antagonistic. It is characteristic that Bremekamp (1956, p. 129) hesitates to class these sporophylls as leaves on account of the fact that they lack axillary buds. The same is of course true for Angiosperm flowers, but in both cases occasional terata betray the foliar nature of these organs, as far as their autonomy goes.

In the phyllosporous groups, notably in the Glossopteridales (*cf.* Plumstead, 1952, 1956), the Ophioglossales¹⁰ and, among the leptoferns, *Aneimia*, a similar unit is apparent, which I would call a *Mixed Bifurcation Unit* (M.B. Unit) since there is no protective function involved. Consequently several auxiliary

¹⁰Both the Ophioglossales and the female coniferous cone have been mentioned by Hirmer (1933) in support to his "Spaltungstheorie".

structures developed in these groups: the sporangia obtained some protection first by their position on the lower side of the frond (I have never come across the case of *Aspidium anomale* (*Polystichum aculeatum*) in which sporangia are occasionally found on the upper side, a case which periodically turns up in literature and which may be based on a single observation) and secondly (in the eusporangiate ferns) by a thickened wall and a coalescence of individual sporangia. The most vulnerable ferns, in this respect, are the Osmundales with their thin and marginal sporangia, and they too, seem about to disappear.

The lepto-ferns *sensu proprio* have often developed super-protective structures of various forms, called indusia. As they always lack nervation, they cannot be ascribed a clear morphological status and while we hesitate to class them as enations, there is no other possibility but considering them organs *sui generis*, the ultimate refuge of morphological terminology. Yet these indusia have repeatedly been compared and even homologised with the integuments of Phanerogams.

Before entering upon this subject, however, we have to point out that the principle of a protective aggregation is not restricted to fertile organs. Vegetative buds are also tender and vulnerable organs and it is not at all surprising that on this basis the same principle got a firm foothold in the vegetative sphere; it resulted in the axillary relation of leaf and lateral axis in all Phanerogams, and I propose to simply call them *Sterile Protective Bifurcation Units* (S.P.B. Units). They seem to corroborate the interpretation of the flower as a modified shoot. As to the peculiar mode of branching of the Sphenopsida, i.e. between and somewhat above the leaves, this could be an example of a sort of "diagonal" dichotomy, due to the unusual venation in the nodes of the stem. Its protective value seems questionable though not entirely lacking. Dichotomies at various angles are well known in the stele (*cf.* Zimmermann, 1956).

The assumption of these Sterile Protective Units as an actual evolutionary tendency explains why in the beginning of this paper, I ventured to make the statement, perhaps surprising to some readers, that in fact all ramifications are primarily dichotomies. It is one of the implications of the recognition of the fact that even in the Angiosperms stem and leaf are not absolute notions. In fact, many terata are more logically explained on

the basis of the assumption that, even in the Phanerogams, sterile and fertile, as well as male and female, are interchangeable (e.g. ovules or microsporangia on a *Ginkgo* leaf), rather than by indulging in speculations on the nature of the leaf as a sporophyll.

Let us now return to indusia and integuments and consider in how far the assertion of their homology is tenable. Integuments are only found in the female sex (unless the envelopment of the stamen in *Najas*, called a perianth or spathella, should be called an integument), and as soon as a megasporangium is enveloped in a special cover (integument) it is generally referred to as an ovule. In a way we could call an integument a super-protective organ but as we shall see later there will follow several others of these.

In the older plants integuments were already of at least two types, that of the Pteridosperms and that of the Cordiales, etc., the former apparently somewhat older than the latter. Initial stages, phylogenetically speaking, are unknown in the first-named type, of which the oldest representatives are already highly developed, the megasporangium being enclosed in an integument which is partly adnate to it and which, in its turn, is surrounded by another cover, mostly lobed and not rarely of specialised construction, called the cupule. There is, however, little doubt that both cupule and integument are of essentially the same nature and origin; both are provided with a well-developed vascular system, often repeatedly dichotomised. Not long ago a still more elaborate structure (*Calathospermum*) was described by Walton (1940) in which a number of bitegumented ovules, some on long, others on short stalks, were together enclosed by a number of lobed, partly connate sterilia, a sort of super-cupula which seems to foreshadow the later perianth and, in a way, even the capitulum of the Compositae, an example of the periodically reiterative process of protective structures on ever higher levels and ever more complicate build (*cf.* Gaussen's (1947) pseudocyclical evolution).

As has been intimated by Walton (1940, p. 134) and Florin (1951, p. 382) this type of tegmentary protection is most easily explained by assuming that the megasporangium originally formed part of a ramification system of which the sterilia arranged themselves either in a cup-shaped structure or, as is more likely on account of the fundamental dichotomy, in (mostly two)

Ginkgo-like "leaves" in which the telomes planated and webbed. This type is in recent plants still represented in *Cycas* whose vascular supply (Gaussen, 1946, p. 47) is in fact hardly different from that in the Pteridosperms, though the cupula (outer integument) is more perfectly connate with the ovule than is the case in the Pteridosperms. The two integuments and the nucellus (megasporeangium) are still more completely welded in the Zamiaceae (*Bowenia*, see Kershaw, 1912) but here too there are two layers of vascular bundles each with many dichotomies.

It is questionable whether the ovule of *Ginkgo* is fundamentally of the same type as that of *Cycas*. In outward appearance and size the two are much alike but there are only two opposite vascular bundles in what seems to be the only integument. When trying to bring the ovule of *Ginkgo* in line with that of the seed-ferns and the Cycads, there are two possibilities: 1. the inner integument has lost its vascular supply and got so completely connate with the megasporeangium as to become beyond recognition, and 2. the single, bivascularised integument is homologous with the inner one of *Cycas* and the annular rim at the base of the *Ginkgo* ovule is the remainder of the outer integument of *Cycas* and the cupula of the seed-ferns. Incidentally I wish to remark that the annular rim in *Ginkgo* ovule, unvascularised as it is, strongly recalls those structures which are generally known as arilli (*Taxus*; Angiosperms).

The second type of integument is much simpler, often unvascularised and bivalved. It is first found in *Cordaianthus* and *Trichopitys* (Permo-carboniferous) and later on in the primitive Conifers. Florin (1951, p. 314) discovered some trace of its possible origin in *Cordaianthus zeilleri* ovules in which the megasporeangium had failed to develop or to develop fully and in which the two-lobed "integument" was still provided with vascular bundles, one in each lobe. So far as I know, however, this is the only indication besides *Ginkgo* in the stachyosporous Gymnosperms that the integument has originally been vascularised.

Besides in the Cordaitales and *Trichopitys* the type just described is apparently also found in the Coniferales, Taxales (arillus as a specialised integument?), Cycadeoidales, Pentoxylales and Chlamydospermales, but in these the supposedly original bivalved condition has hardly left any traces. De Haan (1920, p. 281), of whose work I will speak later, says that in *Taxus*

the arillus is occasionally two-lobed and Roth (1957, p. 231) mentions "Integumentformen der Angiospermen, die mehrzipflige Ränder aufweisen" and thinks that this is significant in view of a telomic origin of the integuments.

Curiously enough, the younger Pteridosperms and *Ginkgo*, so far as known in this respect, take some sort of intermediate position. In *Caytonia* and *Umkomasia* the impression is that there is only a single, perhaps bivalved integument and that additional protection is provided for, not by a second integument, but by the ovule being partly or entirely enveloped in a structure perhaps of leafy origin, more or less comparable to the sporocarps of *Marsilia* (which, of course, has megasporangia, no ovules). *Ginkgo*, on the other hand, is a somewhat doubtful case in view of its mixed relationships: leaves like those of some ferns, strobili like those of *Trichopitys* and some ancient conifers, ovules like those of *Taxus*, and sarcotesta like that of *Cycas*.

Most remarkable and, in a way, leading up to the condition of the Angiosperms, are the Chlamydospermales. Recognising that the three genera, *Ephedra*, *Gnetum*, and *Welwitschia*, however diverging, are all of the same fundamental type, the least specialised case is that of *Ephedra*. In all of the three genera the innermost integument, here called int. I, has been allotted a special function, viz. that of a pseudostyle, fitted out on a gymnospermous level (nucellar pollination drop), capable of catching the microspores. In *Welwitschia* there is only one more integument (II) on the axillary ovule and this has been given a function in the dissemination process in maturity. In *Gnetum* we find integuments II and III, neither apparently with any other function but that of mere protection.

In *Ephedra*, however, there seems, in some cases at least (*E. altissima* (cf. Wettstein, *Handb. Syst. Bot.*, 4th ed., 1933, p. 526, fig. 346) to be no clear limit between successive pairs of "leaves" and integuments. The former get more and more connate and amplexicaulous along the axillary shoot until they completely merge into each other to form what is recognised as an integument as soon as the vascular bundles have disappeared. Accordingly the lower pairs have been called—inappropriately, I think—"bracteoles" or "prophylls", the next "perianth" and the upper two or three whorls integuments. To my mind they are all of the same fundamental type and it is comprehensible

that this very interesting and significant condition is precisely found in a class in which the leaves are essentially decussate.

A corresponding situation is found in the Taxales (*Amentotaxus*; see Florin, 1951, p. 375), but in all other groups with similar, bivalved integuments, in which the phyllotaxis is helicoid (or as it is usually, but incorrectly, termed, spiral) the opposite or whorled arrangement is only found in highly condensed shoots at both ends of the plant, the cotyledons and the integuments.

If these considerations contain some truth and if the conclusion is justified that fundamentally there is no difference between (reduced) leaves and integumental valves, another long-cherished demarcation between Gymnosperms and Angiosperms, that of naked and covered seeds, falls to pieces. And since even in the anatomy (*cf.* also MacDuffie, 1921), as well as in the development of the double fertilisation there are, in *Ephedra* and *Gnetum*, intermediate conditions which may explain the origin of a double fertilisation and of a secondary endosperm as a natural consequence of the (orthogenetical?) reduction of the female gametophyte, whereas the forming of an endosperm, so far as known, shows some range of perfection, there is no single character left to distinguish between Gymnosperms and Angiosperms but the perfect double fertilisation and the secondary endosperm (Lam 1951, p. 394 and 1952, p. C. 78). For, if some outer whorl around the ovule can be considered an integument as well as a perianth, both Hagerup's interpretation (1934) of the coniferous integument as a phyllome and his pseudocarpels in Angiosperms in which the ovules or ovule (*Myrica*, *Chenopodium*, *Amaranthus*, etc.) are, I presume, axis-borne and enclosed in an "ovary", built up of two phyllomes, as well as the often-pronounced interpretation of the annular rim in the *Ginkgo* ovule as a reduced "sporophyll", fall into place and only the terminology has to be corrected and brought in line with those of, say, the Ephedraceae.

Recently the Indian botanist Majumdar (1956) in a most interesting discussion on carpel morphology, which only came to my knowledge after I had almost completed the present paper, arrived at a similar opinion which is very close to my views indeed. It seems appropriate here to quote the last point of his summary: "The ovule is a terminal sporogenous structure (megasporeangium) on the funiculus (stalk), and thus equivalent to the

determinate terminal bud surrounded by annular outgrowths which may be likened to the perianth segments or tubes”.

I have at times indulged in combining the Verticillatales (*Casuarina*) with the Chlamydospermales into the class of the Protangiosperms, mainly on account of their whorled arrangement and their solitary, sometimes bifid, stamen. In view of the above reasoning, however, this classification is somewhat weakened by the female *Casuarina* flower which is clearly more advanced even than that of several Monochlamydeae in so far as the (pseudo) carpels are entirely connate, forming an essentially two-celled ovary and two long, free styles, whereas only one of the participating carpels forms a mixed protective bifurcation unit with a fertile dichotomy with two ovules, each with two integuments. In addition, *Casuarina* is reported to have pollen of the type of the Amentiferae and to possess endosperm in the seed; and so long as the last-named character proves to be differential enough, I think we had better return to the traditional opinion and, dropping the Protangiosperms as a class, reinsert *Casuarina* in the Angiosperms. In view, however, of the above conclusions regarding the integuments and the pseudo-carpels, it must be emphatically stated that the difference between gymnospermy and “Gymnosperms” on the one hand, and angiospermy and the “Angiosperms” on the other, has again shrivelled up. In fact, only the double fertilisation and the occurrence of secondary endosperm so far stand as differential characters and it is not impossible that even they will fade away on closer investigation. Meanwhile, typologically speaking, the Chlamydosperms are clearly closer affiliated to the Angiosperms than to any known group of Gymnosperms. The term “flower” which has, elsewhere in the present paper, been mentioned as a typical Angiosperm feature has, however, gradually lost all morphological significance and is at best an expression of some biological consequence.

In addition to this, I have to say a few words on the integuments of the Angiosperms. Of these there may be one, or two, or even more, including several types of arilli. In a few of these (Urticales, see Eckardt, 1937) vascularisation is known and, remarkably enough, not the simple type of a bundle for each valve (if any) but a dichotomised system like that in *Cycas*. Warming, in his synoptic paper of 1913, mentions vascularised

integuments in many more families, all to be considered primitive and both stachyosporous and phyllosporous, but he homologises them (with doubt) with the fern indusia. In general, I see little correlation between the types of ovules on the one hand and stachyosporous-phyllospory on the other, but this may be partly due to our still very imperfect knowledge of both subjects; and immense fields of problems have to be explored before we can expect convincing, let alone conclusive data to solve them.

However this may be, it seems hardly dubitable that the inner integument is to be considered the outcome of a specialised telome system and it is comprehensible that this should have arisen in more than one way. The same, however, is likely to be true for the other integuments. Whereas the inner one seems to have obtained a special function in the Chlamydospermales, the outer ones appear to have had a better chance for various functions: arilli of some types and functions, and in some cases perhaps even pseudo-carpels or a "perianth" of some description are to be interpreted in this light (see Roth (1957), who states that "sich sogar Perigonblätter und Integumente desselben Wachstumsrhythmus zu bedienen (scheinen)", p. 224). In this context Miss Roth need no longer worry about the origin of the second (outer) integument of *Capsella* (or any other Angiosperm) even though it appears later in ontogeny than the first one. Melville (1957, p. 299) suggests that it may be due to a process of "repetitive evolution", a rather meaningless expression if the process should be considered in line with e.g. the formation of consecutive leaves on a branch. However that may be, in a very old and at the same time specialised organ like an ovule, of which the nucellus might well represent an original telome, it would be claiming too much to be able to distinguish between "stem" (funiculus) and "leaf" (integument) in the angiosperm sense and to expect that they should behave like axes and leaves in the vegetative area. I fully agree with most of Roth's conclusions, notably where she says that the "integument" of *Azolla* can hardly be anything else but an analogue of the Angiosperm integument: typologically there is not the slightest connection.

Roth recalls that regarding the interpretation of integuments several theories have been proposed. Next to the rejected identification as enations, they are referred to as the bud theory (Schleiden), the leaf-theory (Celakovsky), and the *sui-generis* or

sporangium theory. In spite of her generally unbiased views, Roth is obviously still under the spell of the old morphology concept of the three basic organs, stem, root and leaf. For, since on account of our present knowledge it is obvious that the sporangium-theory is the only valid one, she points out (p. 212) that this would mean "dass sie (the ovule) als morphologisch weiter nicht definierbares Organ gelten muss, also mit den drei Grundorganen der Pflanze nicht zu homologisieren ist". Yet, she states later (p. 229) that "sich gegen die Sui-generis-Theorie . . . verschiedene schwerwiegende Argumente ins Feld (führen lassen)". This is comprehensible, since Roth has studied histogenesis and since her own conclusions are morphological rather than phylogenetical. Ultimately, however, she admits that phylogeny will probably have the last word and though still somewhat reluctantly she accepts the views published by Zimmermann, Florin and others, briefly summarised above in the frame of my own experience. Chadeaud (1946) in his study on the origin and the evolution of the Phanerogam ovule, arrives at similar conclusions, but to my taste he clings rather too much to the leaf-autonomy concept and takes the Angiosperms too much as a point of issue in so far as he, for instance, compares the integuments with "leaflets" of the (compound) sporophyll. It must be admitted, however, that he enumerates some possibilities and quotes opinions of other investigators rather than proposes a theory of his own.

In this context it is interesting to take cognizance of a publication which is almost forty years old, the doctor's thesis of H. R. M. de Haan, one of the late J. C. Schoute's pupils, and a man who unfortunately shortly after his promising start in botany switched over to the medical study and profession and is now a practising physician in the same town in which the present paper is written. De Haan's work (1920), which is often found quoted, is still worth while reading and was, in fact, well in advance of his time. His conclusions were:

1. The integuments of the Pteridosperms and Gymnosperms are homologous and most probably also homologous with those of the Angiosperms.
2. The integuments are not homologous with the indusia of the Ferns and Lycopods, and the first name may not be used for these organs.

3. The integument is originally composed of Units.
4. The value of the units is not yet quite certain."

I think that these conclusions are remarkably clever. De Haan has anticipated many of the present views, even the concepts of stachyosporous and phyllosporous, though his trend of thoughts on account of his subject kept him from giving them proper expression

In spite of the somewhat obscure wording of De Haan's conclusion no. 2, the modern phylogenist can well approve of the four theses. The "units" mentioned in 3 and 4 can now be indicated with some likelihood: they are either telomes, or syntelomes or reduced syntelomes (see Lam, 1952, fig. 6, p. C. 64).

In our above considerations about the protection of such vital organs as megasporangia, we stuck at the integuments, only mentioning such superprotective organs as the supercupula of *Calathospermum*. So, to complete the picture we have to recall that in the higher groups this process of superprotection still went on. Whereas in the Ginkgoales and the Cycadales-Cycadaceae no additional superprotection has been brought about, in the (phyllosporous) Cycadales-Zamiaceae and the (stachyosporous) female strobili of the Cycadeoidales an additional protection is obtained, in the former by a process of condensing the strobili and shifting the ovules underneath a peltate sterile part of the sporophyll, and in the latter by the formation of a sort of (sometimes bisporangiate) "flower" which seems to foreshadow the later Angiosperm flowers; the Angiosperms are distinguished from, say Cycadeoidea, in that the ovules are not interspersed with sterile organs and are enclosed by pseudocarpels or true carpels. The Pentoxylales have not developed a special superprotection except for the close aggregation of the ovules into a compound co-ovulanium.

In the Conifers, as in the Lycopsidea, though on a higher level, superprotection has been effected by the often tight enclosure of the megasporangium-bearing shoot in the axil of a phyllome.

In the Chlamydosperms and the Angiosperms we meet with at least two new types of superprotection: in the first of these (the stachyosporous type) some arillus-like, or integument-like cover of two or more sterile whorls shifts upward and encloses (as pseudocarpels) the axis-borne ovule or ovules; in the second one (the phyllosporous type) the ovules are inserted on sporophylls

which enclose them by a process of infolding. It will require a great deal of work to find out where, in the Angiosperms, the line between the types, if existing at all, is to be drawn. With full recognition of Eckardt's (1957) painstaking attempts to find out whether some Monochlamydeae may be considered stachyosporous or not, I am not sure that he has succeeded in freeing himself from all bias, which, indeed, seems to be exceedingly difficult for an investigator who all his life has studied living tissues. The phylogenetical trend of thought is a historical and comparative one and it can only be acquired by thinking along its lines for years and years.

Even though we are entirely ignorant of how and when, this much can be said, that through the two types of superprotection just described the Angiosperms developed into what they are now. The process was accompanied by the formation of "flowers", complex structures of various origin and enormous diversity, brought about by the accumulation of phyllomes, or axes, or both, of varied shape and function; structures which are primarily, like the leaf, biological (functional) rather than morphological units; structures that might form the only character in distinguishing the Angiosperms if only we were able to say what they are, how to describe them and to state when a flower is still worthy of that name. Perhaps the Angiosperm flowers are, indeed, still much more complex than has generally been surmised on the basis of the pseudanthium-theory, and Nozeran's remarkable and interesting expositions (1955) are well worthy of careful consideration.

The process of protection of the most vital part, the ovule, went on. While on the one hand, various structures arose which furthered pollination, on the other the ovules were more and more closely enveloped in thick-walled ovaries (formed by one or more (free or connate) carpels or pseudocarpels); these ovaries again, were in their turn, covered up by tissue of doubtful origin, a process resulting in the inferior ovary. Perhaps the aggregation of flowers into inflorescences, and these again into super-inflorescences form part of the same process, whose essence is the protection of future generations. The whole of it is covered by what Gaussen (1942-1952) has termed "pseudocyclical evolution" in connection with the concept of "surévolution" (super-evolution).

Throughout the system of the land plants, from the Cambrian

to the present day, from the very time that the first aerial sporangium was lifted out of the waters, this fundamental organ has remained what it was in the very beginning: a fertile telome. In my opinion it still is. A megasporangium, whether or not enveloped in one or more integuments (and then called an ovule), whether inserted on an axis (whatever that may be) or on a leaf (whatever that may be) is still a terminal sporangium, its funiculus is provided at best with a protostele, and it may be long or short or non-existent. A microsporangium, whether solitary or in unison with one or more others, whether inserted on an axis or on a (deceivingly reduced axis-like) leaf, still remains a fundamentally terminal sporangium, only pushed aside by its associates or connected with them in dichotomies. In fact, the Angiosperms are, as it were, full of tiny *Rhynias*, everywhere, in their leaves and in their flowers, in their vegetative and in their reproductory parts, and this links them in a most fascinating way with their ancestors which first ventured to shed their spores in the air.

Probably in close association with the processes depicted in the above, are those governing the vicissitudes of the gametophyte. Somewhat earlier in the present paper I alluded to its orthogenetical nature. There is, in fact, something uncanny, about the steadfastness with which the female gametophyte diminishes in size and differentiation, losing its physiological independence, gradually seeking cover and protection as it decreases and gets more vulnerable, yet with incredible tenacity clinging to some sort of aquatic environment, creeping away in the tissues of the sporangium, the latter again hiding deeper and deeper in the body of the mother plant, until the size of the gametophyte gets so much reduced as to be no longer capable of feeding the young embryo and shifting over to the resources of the diploid mother plant becomes a vital necessity. A development singularly reminiscent of that other grand process in vertebrate animals which ends in the mammals whose embryos in a comparable way are parasitising on their mothers.

A most peculiar rôle in the evolution of the gametophyte is played by the ventral canal-cell, next to the egg-cell, the one which shows the greatest resistance against abolition. If the polar cells in the embryo sac are to be homologised with the ventral canal-cells of two archegonia in Angiosperms, in the very nick of time

the ventral canal-cell, after some preparatory training in the Chlamydosperms, managed to learn the trick of copulation (after a virginity of some hundreds of millions of years), thus betraying itself as a potential egg-cell and giving rise to a new nutritional tissue on behalf of the young sporophyte; rather too late, however, since the space available greatly reduces the nutritional capacity of the endosperm and the young embryo has very soon to appeal to the nutritional equipment of the old sporophyte. Should this line of development be pursued it may lead to the reduction of the entire gametophyte but for the only really vital cell, the egg-cell. In that case the Angiosperm life-cycle would have reached the same level which has already been long attained by *Fucus* and by the animals.

Phylogeny is like Morphology, Old and New, simple in its general lines, extremely complicated in its details, at least so it seems to us. In the above we have made an attempt to sketch some of the traits of, as H. J. Muller (in Jepson, Mayr, and Simpson, 1949, p. 421) puts it, "the great complex beast called Life . . . (which) . . . has left behind him a long and devious though often ill-marked trail". In order to follow its footsteps, we had to dig deep into the past but on interpreting what we came across there we were hampered by prejudices, dazzled as it were by the clear-cut images around us in the sharp light of the present. It is like the intuitive hesitation of the swimmer before taking a dive into a dark pool of unknown depths, closing his eyes and afraid of an uncertain aim.

It is our impression, not to say, conviction, that in tracing the origin of present groups as well as of organs and structures, we have to dig deeper than we have done so far. Again and again we are forced to admit that we have rashly and prematurely stopped in the opinion that we had arrived where we wished to be, and once there, we gradually realised that our actual aim lies still farther away.

The differentiation between sterile and fertile probably lies at the very roots of Life and was, of course, in the land plants, already of accomplished inheritance. Heterospory has most probably developed in the earliest stages of land life, even before the first telome-leaves were shaped. This was obviously meant by Darrah (1939) when he wrote (p. 99): "The seed may in fact be

older than the leaf". The development of heterospory clearly took place several times independently.

As to the relationship between stem (axis) and leaf we have, in the above, repeatedly hinted at our opinion that their autonomy, particularly in the Phanerogams, has mostly been grossly overrated. Our impression is that the period of differentiation of leaves from stems must have been a very long one, and the conclusion is justified and even inevitable though insufficiently recognised, that even in the Angiosperms interchangeability and intermediate types are to be expected, particularly in flowers. In connection with the assumption that a similar interchangeability exists between sterile and fertile, this may be the principal cause of great and seemingly unbridgeable controversies in the interpretation of certain flower parts, notably stamens, carpels, and integuments. While the metamorphosis theory of the flower may be considered valid for many flowers, there may be some reason to doubt it concerning others. This applies not only to my own concepts of stachyosporry and phyllosporrry but also to such extreme views as those of McLean Thompson, Grégoire (1931, 1938), and Plantefol (1949) (all anatomical-histological-morphological theories rather than phylogenetical ones) as well as to the interpretation of certain flower terata, if only we realise that organs which are neither clearly stems nor leaves may have arisen very early in evolution, having retained their intermediate position up to the present day in which they became more and more pronounced as the extremes themselves—stem and leaf—gained in autonomy. Majumdar (1956) considers the possibility that carpels, or some carpels may be organs of such an intermediate nature.

I would, however, not go so far as Maekawa (1952) who extends the concept "leaf" even to fertile axillary structures and I am afraid that the ideas expressed in his fig. 18 (p. 19) are confusing in so far as male and female axillary structures of (the stachyosporous) *Ginkgo* are compared to male and female sporangia of a dicotyledonous plant (*Austrobaileya*) of a clearly phyllosporrrous nature.

In conclusion, a few words on another confusing topic, homology, about which much has been written and little is understood. One thing, however, is certain, and it has been very well worded by Grégoire (1931, p. 1289): "l'on ne peut pas définir une notion

phylogénétique de l'homologie qui n'ait son fondement dans la notion ontogénique". Mason (1957) expresses himself in similar terms and though making an attempt at a modern definition of the concept on the basis of a system covering both the cell division hierarchy and the differentiation hierarchy, he failed to bridge the gulf between the present and the past, the unsurmountable barrier in all sciences dealing with time.

It is true that the solution of phylogenetical problems can be furthered by meticulous investigations on recent plants, including the biochemical and genetical background of morphogenesis (see Turing, quoted by Melville, 1957); it may be admitted that "morphological equivalence" (Mason, 1957, p. 87) is a less-burdened term for homology, the fact remains that a clear understanding of the concept tends to escape us. Yet, though we fail in giving a definition, everybody concerned is sure that homology is real and everybody attaches his own meaning to it.

To my mind one of the causes of this situation is that homology and analogy are gradatingly connected, neither being fully itself. Another cause is that homology presupposes genealogical kinship and even if we would be in a position to trace the latter, we would at the same time have to realise that kinship is not rectilinear but reticulate. "The basis of homology rests in the identity of structure, and implies origin from a pre-existing similar structure", says Mason (1957, p. 91). Here I agree; but everything beyond the homology of two daughter-cells after a cell-division largely rests on intuition and belief.

Meanwhile Boyden's paper (1947) on the subject is well worth reading. He gives a clear historical survey of the concept from a zoological viewpoint and usefully distinguishes between three types of homology: 1. general homology (the principle); 2. serial homology or homotypy (comparison of various organs of the same individual or rather life-cycle); and 3. special homology or homophylysis (comparison of organs of different individuals or taxa). Approaching the problem from a genetical rather than an ontogenetical side, he states that the term analogy is not to be considered opposite to homology; it is rather the lack of homology and, if necessary, cases of this type are to be described as non-homologous, or convergent, or parallel. From the fullest recognisable homology, described primarily as structural correspondence, and secondarily as based on common ancestry, the

transition to the fullest recognisable non-homology is gradual. However, since we cannot deny that the root of the problem lies in ontogeny, the question is: can we proceed beyond the observable ontological facts and proceed to the benefit of a better insight as to what homology actually is?

As I have explained in the above, I think we can if we keep ourselves in hand in accepting some uncertainty. As we have seen, it may be suggested that vascularisation gives us some hold in the recognition of the origin of organs in land plants. The orientation of vascular bundles provides some support in distinguishing stems and leaves (such as the ovuliferous scale and the bracts in the female coniferous cone) but in other cases this character fails us, e.g., in many floral organs. All this with the reserve that vascular bundles, being functional structures, need not always betray phylogenetically earlier conditions (Puri, 1951). The capriciousness and relative untrustworthiness of anatomy and ontology towards phylogenetic conclusions, at least in Angiosperms, in some cases confidently used as evidence, in others rejected as insignificant, is shown by the fact that leaves are externally developed from the tunica of the growth point and are only later on connected to the stele by vascular tissue. If taken seriously this might be used as a proof against the syntelomic origin of the leaf and I think that few phylogenists are prepared to go that far.

A slight indication of the way in which biochemistry may be of assistance to phylogeny has recently been given by Melville (1957, p. 294) who suggested that rhythmic alterations ("waves") in metabolic substances cause regularly occurring isotomous dichotomy, presuming that anisotomy be caused by inequality in these processes in the growing point. This is not exactly surprising, but it is interesting to note that apparently the process falls within the scope of the experiment or begins to do so. Similar processes are suggested as happening regarding growth differences and alterations as discussed above, resulting in shortening and aggregation of parts, due to either growth stimulators (hormones) or growth inhibitors. In hybrids these two may counteract each other, resulting in a failure of the organ in question (e.g. deleted leaves), or intensify the activity, leading to an exaggerated growth (e.g. in leaf margins of such ferns as *Pteris*).

Bouillenne (1955) gave a clear survey of the biochemical side of the problem, showing that hormones are responsible for the formation of organs, including floral organs. Nothing is known, so far as I am aware, of the genetical background of these enormously complex processes but it is certain that they lie at the very basis of differentiation. In view of the probability that they are more complex in the higher Cormophyta than in the lower ones, it might be suggested that the processes, determining the differentiation sterile-fertile, be investigated on such plants as *Psilotum* (which is easily cultivated and even runs wild in green-houses), *Lycopodium*, *Selaginella*, and ferns. It seems likely that in these groups, in which the sporangia are not preceded, surrounded, and encumbered by so many auxiliary organs, that differentiation is happening in fewer stages, by simpler means, and in a shorter time than in higher ones.

But even if these processes would be known to us, there would still be the mystery of the sequence of ontological events from the zygote and the embryo, in which differentiation must be necessarily downright stormy, through adolescence to full maturity; a sequence which is probably one of the most characteristic features of the condition called Life and of its material manifestations, the organisms.

At any event, further investigations along these lines seem promising and may contribute to bringing phylogenists and ontogenists together, thus enabling them to co-operate to the benefit of a better understanding of what the four-dimensional plant world actually is.

SUMMARY.

Some questions discussed in and conclusions arrived at in the above paper are:

1. Paleobotany changed the face of Morphology.
2. Did Life develop out of the inanimate world in one single period or has it done so continually?
3. Did the taxonomic "levels" (categories of increasing size and discontinuity) now recognised rise at one given period, or do they continue to widen their scope?
4. Why are "intermediates" in paleontology so rare?
5. Two elementary processes in the evolution of plants are: (more or less slow) growth alterations and (more or less sudden) differentiation.

6. Differentiation primarily arises from unequal cell-division; growth changes are functions of tissues (meristems), due to physiological causes. Both are genetically determined.
7. The concept of homology rests on inequality of daughter-cells of a cell-division and, though more vaguely, on the comparison of organs to which growth alterations are ascribed (*cf.* point 28).
8. The concept "leaf" has no morphological basis; at best it is a functional notion (*cf.* point 20).
9. The basic unit in the Cormophyta is the protostelic telome. In all but the most primitive types, all nerves are homologous with mesomes, nerve endings with telomes or mesomes. Most organs can only be interpreted as homologa of other organs when at least some of them are vascularised.
10. Dichotomy is the only and universal way of ramification in Cormophyta except perhaps in the very oldest ones. The possibility of an original lateral ramification is discussed. Types of ramification, traditionally described or named differently are derivable from the original dichotomy by the assumption of some simple evolutionary processes to which can be ascribed a selectional value.
11. Mixed Protective Bifurcating Units (M.P.B. Units)—a dichotomy with a fertile and a sterile part—arose early in the evolution of stachyosporous Cormophyta and acquired a considerable autonomy. They were either mono- or poly-telomic, resulting in the axillary position of sporangia in the lower groups, as well as in the "Schuppenkomplex" of the female Coniferous cone and axillary stamens and ovules (or placentae) in stachyosporous Angiosperms. M.P.B. Units are characteristic of stachyosporous groups and relatively efficient. In these groups overtopping was an early prevailing principle in the reproductive sphere; in the vegetative one (main ramification) dichotomy was preserved in some groups (Psilopsida, Lycopsida).
12. Similar units, though not protective, are found in the Ophioglossales as well as in such lepto-ferns as *Aneimia*. They are here called Mixed Bifurcation Units (M.B. Units). They are the basic type in the phyllosporous groups, in which the dichotomies were (and are) long preserved, both in the vegetative and in the reproductive spheres; overtopping is

acquired much later and mainly in the vegetative sphere. The intrinsic protective power of the M.B. Units is weak and had to be improved by several auxiliary structures (*cf.* point 14).

13. The association of leaf and axillary shoot is based on the same principle as is valid for the M.P.B. Units. In the first-named case we may speak of Sterile Protective Bifurcation Units (S.P.B. Units). They confirm the interpretation of the axillary flower as a modified shoot. It is conceivable that in both types correlative processes have developed, by which the two components influence each other physiologically. The latter process is supposed to occur in the cones of both sexes in Cycadaceae, and the male ones in Coniferae, in which the sporophylls are not known to produce axillary buds, sterile and fertile being known to be antagonistic. In younger Sphenopsida a diagonal S.P.B. Unit is found between leaves and branches, based on the peculiar venation of the node.
14. Other types of protection were acquired in the phyllosporous ferns, such as position of the sporangia on the lower leaf side (except where the leaf is infolded, as is the case in *Marsilia*), forming of thick-walled synangia (eusporangiate ferns) and indusia (leptosporangiate ferns).
15. It is stated that superprotection of megasporangia was first obtained at an early period by the development of one or more integuments and that these integuments have originated by the shifting upwards of sterile telomes or syntelomes, often two of them, as is intimated by the venation of several integuments.
16. Two types of integument are recognised: the type of the Pteridosperms and the Cycadales with dichotomising nerves, and the type of the Coniferopsida, Cycadeoidales, etc., which is bivalved and mostly not vascularised. In several ways, *Ginkgo* takes an intermediate position.
17. There seems to be no or little correlation between the two integument types on the one hand, and stachyosporophyllospory on the other.
18. A megasporangium covered by an integument is called an ovule. It is suggested that integuments belong to the same morphological category as the cupule of the Pteridospermales, arilli in many groups and, in some cases, pseudocarpels.

19. In some *Ephedra* species the pairs of decussate leaves on the axillary female shoot gradually merge into what has sometimes been called perianth, sometimes outer integument. It is suggested that the series is continued up to and including the innermost integument.
20. It is further supposed that the same condition is to be found in some Monochlamydeous Angiosperms with "false carpels" (pseudocarpels) in which case another distinction between Gymnosperms and Angiosperms is fading away, the only remaining ones being the double fertilisation and the ensuing secondary endosperm, characters which, like the others, may prove to be of doubtful differential value. The concept "flower", having no objective morphological status, is accordingly differentially useless and should not be used as a botanical term (*cf.* point 8).
21. Under these circumstances *Casuarina* had better be reinserted in the Angiosperms and accordingly the Protangiosperms as a class dropped.
22. Superprotective structures are of several kinds and levels: the supercupula of *Calathospermum*, peltate and closely congregated sporophylls in the Zamiaceae, close aggregation of ovules and interspersed sterile organs in the Cycadeoidales, of ovules in the Pentoxylales, of Mixed Protective Bifurcation Units in the female coniferous cones, Chlamydospermales and stachyosporous Angiosperms, infolding of sporophylls in phyllosporous ones, inferior ovary in both, aggregation of flowers into inflorescences and of these into superinflorescences.
23. Sporangia of both sexes have, like the sterile telomes, retained their original autonomy in whatever way they are secondarily grouped, arranged, or protected.
24. With the progressive evolution of the sporangia, the regressive one of the gametophytes goes hand in hand. The peculiar rôle played by the ventral canal-cell is described and the possible pursuance of the line of evolution given in outline.
25. Interchangeability of sterile and fertile "telomes", as well as stem and leaf, is to be expected even in the Angiosperms. It may account for several controversies in the interpretation of organs as well as for that of certain terata.

26. The autonomy of such organs as stems and leaves is mostly overrated. The existence of organs of an intermediate origin should be seriously considered.
27. In endeavouring to interpret present organs and their phylogenetical relations we have mostly to dig much deeper than was originally anticipated.
28. The concept of homology (*cf.* point 7) is discussed again. It is stated that recently attempts have been made to give it ontogenetical implications. Recent investigation in the biochemistry of meristems seem promising in this respect.
29. Anatomical, ontogenetical, and in general static (one-time) data alone can never be conclusive towards the solution of phylogenetic problems, though their evidence may be of outstanding importance when interpreted in a phylogenetic (dynamic) sense.

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THE LARGER FUNGI OF ST. ANDREWS SAND DUNE AND LINKS AREA.

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This study was carried out from the spring of 1952 till the winter of 1957. Its purpose was to collect dune fungi in an area in East Scotland and compare the records so obtained with the known occurrence of dune fungi in Scotland as a whole, in the British Isles, in Scandinavia and in Greenland. The appearance of papers by Hassell (1953) and Wallace (1954, 1956), while the work was in progress, provided lists based on the intensive study of two sand dune areas in southern England and one in eastern Ireland and extended very considerably the information available on British dune fungi.

The occurrence in sand or sandy soil in the British Isles of over 310 species of larger basidiomycete and ascomycete fungi has been recorded by Stevenson (1879, 1886), Phillips (1887), Massee (1892-95), Rea (1922), Ramsbottom (1923, 1953), Dennis (1948, 1952, 1955), Pearson (1949, 1952), Wakefield and Dennis (1950), Ramsbottom and Balfour Brown (1951), Hassell (1952, 1953) and Wallace (1954, 1956). In about 210 of these records the fungi are stated to grow in sand dunes or in grassland near the sea. Of the 33 records which refer to Scotland, 17 are for sand dune or seaside fungi. [Stevenson (1879), Dennis (1948, 1952, 1955).]

Wallace (1954), in his account of the larger fungi at Dawlish Warren, records the finding of 48 species in mobile and semi-fixed dune, naming 7 and 11 characteristic species respectively from the two zones. In the fixed dune (grass and heath land) area of the Inner Warren he found a further 63 species, 7 of which are named in relation to this zone. The species list in the appendix to the paper relates to the Warren as a whole and contains 139 species. Wallace (1956) lists 178 species for South Haven Peninsula, Studland Heath. In the habitats which correspond roughly to those present in the dune and links area at St. Andrews, the numbers of species listed are as follows:—*Mobile Dunes*—9; *Semi-fixed Dunes*—10; *Coastal Heath*—21; (this excludes 5 species which occur "under birch", as this plant is absent from

the area investigated at St. Andrews); *Dune Sward*—55; *Winter Pools*—16 (this excludes 1 species associated with birch and 3 with willow, for the reason given above). The analysis given by Wallace shows that most species are not restricted to one particular zone, though 5 of the 9 *Mobile Dune* species are so restricted.

There are no records of fungi in sandy soil in Orkney. Dennis and Gray (1954), referring to the higher fungi which occur in Shetland, write: "the remaining species, especially the Hygrophori, seem to favour the better-drained soils where grasses prevail over carices, as along roadsides and on sandy flats at the head of bays"; but they do not specify any of the fungi to which this statement refers. Möller (1945) mentions 7 records of species or varieties of *Inocybe* on sandy soil in mountainous areas in the Faroes. He gives no seaside fungi. Christiansen (1941) gives no records of sand dune fungi in Iceland.

Ferdinandsen (1910) made only 1 record of a fungus, *Inocybe lacera*, from sandy soil in Greenland, but Lange (1957) refers to 18 sand dune fungi in Greenland, including this species.

Andersson (1950), in his account of the fungi of sandy grass heaths and sand dunes in Scandinavia, lists 21 species. Lange (1935-40) refers to sandy habitats in connection with 39 species of Danish Agaricales, and specifically to maritime habitats for 14 of these. The two works have 3 species only of sand dune fungi in common (*Inocybe halophila* = *I. lacera* var. *halophila*, *I. serotina*, *Psilocybe ammophila*), so that the total number of Scandinavian records for this type of habitat is 32.

There are nomenclatural difficulties in considering and comparing British, Greenland and Scandinavian records. If, however, the identity of varieties and forms is set aside the three lists have 5 species in common, while British and Scandinavian lists have 16 species in common. This number is made up of 11 agarics, 1 gasteromycete and 4 ascomycetae, viz. *Bolbitius vitellinus*, *Clitocybe aurantiaca*, *Inocybe halophila* (*I. lacera** var. *halophila*), *I. maritima**, *I. serotina**, *Marasmius oreades*, *Nolanea staurospora*, *Omphalia luffii*, *Psalliota comtula*, *Psilocybe ammophila*, *Tricholoma paneolum*, *Phallus hadriani*, *Corynetes arenarius**, *Geoglossum cookeianum*, *Geopyxis ammophila*, *Sepultaria arenicola**.

*Species common to British, Greenland and Scandinavian lists.

The information on the occurrence of sand dune fungi outwith St. Andrews which is summarised in the preceding paragraphs has been extracted from very extensive tables drawn up by the writer and retained in his possession as too bulky for publication.

The larger fungi of the sand dunes and golf links at St. Andrews (map reference 49/18) were collected in the classical locality in which the Rev. M. L. Anderson found *Psilocybe ammophila*, *Tricholoma arcuatum* and *Peziza ammophila* (Stevenson, 1879). All are still present in the area. It extends to 430 acres approximately. It comprises the golf links and dunes lying between the St. Andrews-Guardbridge railway line and St. Andrews Bay. It includes mobile, semi-fixed and fixed dune, dune slack, dune grassland and heath carrying *Calluna vulgaris*, *Erica cinerea*, *E. tetralix*, *Ulex europaeus*, and a considerable tract covered with introduced *Lupinus arboreus*. There are occasional bushes of *Sambucus nigra*, but no *Betula*, *Salix* or *Alnus* species. A large area of made-up ground within the locality was excluded from the survey. This was created by dumping domestic refuse and covering it with soil from a variety of inland sources. It carries large crops of *Coprinus comatus* and other species equally typical of ground rich in organic matter. This fungus flora is quite different from that occurring naturally round about. *Auricularia auricula-judae* occurs on *Sambucus nigra* stems and *Dacryomyces deliquescens*, *Tremella mesenterica* and *Polyporus lentus* on those of *Ulex europaeus*. *Claviceps purpurea* is frequent in the ears of *Elymus arenarius* and *Ammophila arenaria*. These fungi are excluded from the total of 58 species listed below, all of which occur on the surface of the sand or sandy soil. Any connections which they may have with other plants are more or less subterranean.

ST. ANDREWS DUNE AND LINKS FUNGI.

BOVISTA PLUMBEA	CRINIPELLIS STIPITARIUS†
CALVATIA CAELATA*†	CRUCIBULUM VULGARE
CLAVARIA CORNICULATA.	CYATHUS OLLA†
C. PULCHRA	ENTOLOMA SERICEUM†
C. VERMICULARIS	FLAMMULA FLAVA
CLITOCYBE AURANTIACA†	GALERA LATERITIA†
C. DEALBATA†	G. TENERA*†
C. RIVULOSA†	GEOGLOSSUM COOKEIANUM*†
COLLYBIA MACULATA†	GEOPYXIS AMMOPHILA*†
C. VELUTIPES†	HYGROPHORUS CONIUS†
COPRINUS PLICATILIS*†	H. MINIATUS

H. NIGRESCENS†	PEZIZA BADIA
H. PSITTACINUS	PHALLUS HADRIANI†
H. VIRGINEUS	PHOLIOTA PRAECOX†
INOCYBE MARITIMA*†	P. PUMILA var. SUBFERRUGINEA
LACCARIA LACCATA†	PLEUROTUS LONGIPES
LEPIOTA AMIANTHINA†	PSALLIOTA ARVENSIS
L. NAUCINA	P. CAMPESTRIS
L. SERENA	PSILOCYBE AMMOPHILA*†
LYCOPERDON ECHINATUM	P. ATRORUFA†
L. HIEMALE†	STROPHARIA AERUGINOSA†
L. SPADICEUM†	S. ALBOCYANEA
MARASMIUS OREADES†	S. CORONILLA
MORCHELLA ESCULENTA†	S. INUNCTA†
NAUCORIA ARVALIS†	TRICHOLOMA MELALEUCUM† and forma ARCUATUM*
N. SEMIORBICULARIS	T. PERSONATUM and GLAUCOCANUM
OMPHALIA FIBULA† var. SWARTZII	T. PANEOLUM†
O. PYXIDATA†	TUBARIA FURFURACEA
O. RUSTICA	T. INQUILINA†
O. UMBELLIFERA†	T. PELUCIDA†
PANAEOLOUS CAMPANULATUS†	
P. FIMICOLA† var. ATER	

*=recorded previously for Scotland. †=recorded previously for the British Isles.

Fifty-four of the St. Andrews species do not seem to have been recorded on dunes or links in Scandinavia and 23 have not been so recorded for the British Isles. These carry no special mark in the list above. Eight of the 23 occur in the true dune area, viz., *Crucibulum vulgare*, *Omphalia rustica*, *Peziza badia*, *Stropharia albocyanea*, *Clavaria vermicularis*, *Flammula flava*, *Pleurotus longipes* and *S. coronilla*.

Seven of the 14 fungi common to British and Scandinavian lists occur at St. Andrews, viz. *Clitocybe aurantiaca*, *Geoglossum cookeianum*, *Geopyxis ammophila*, *Inocybe maritima*, *Marasmius oreades*, *Phallus hadriani* and *Psilocybe ammophila*.

There is no precise distinction between mobile and semi-fixed dune at St. Andrews. Fungi of the combined region number 9, viz. *Cyathus olla*, *Geopyxis ammophila*, *Omphalia pyxidata*, *Phallus hadriani*, *Psilocybe ammophila* and *Tricholoma arcuatum* (*mela-leucum*), which have been recorded by Hassell or Wallace for this type of habitat, and *Inocybe maritima*, *Pleurotus longipes* and *Peziza badia* which have not. Fixed dune of the rest of the true dune seaward of the golf links, carries 31 species. *Clitocybe dealbata*, *C. rivulosa*, *Crinipellis stipitarius*, *Cyathus*

olla, *Entoloma sericeum*, *Galera tenera*, *Geoglossum cookeianum*, *Hygrophorus conicus*, *H. nigrescens*, *Lepiota amianthina*, *Lycoperdon spadiceum*, *Naucoria semiorbicularis*, *Omphalia fibula*, *O. pyxidata*, *O. rustica*, *O. umbellifera*, *Panaeolus fimicola* var. *ater*, *Stropharia aeruginosa*, *S. coronilla*, *S. inuncta*, *Tricholoma melaleucum* and *Tubaria pelucida* have all been recorded by Hassell or Wallace for this type of habitat. The following 9 species have not: *Coprinus plicatilis*, *Cortinarius caesiocyaneus*, *Crucibulum vulgare*, *Galera lateritia*, *Naucoria arvalis*, *Pholiota praecox*, *Clavaria vermicularis*, *Flammula flava* and *Stropharia albocyanea*.

Eight of the 17 species previously recorded as sand dune fungi in Scotland have been found at St. Andrews. The present work has increased the number of Scottish records from 17 to 71. This total is made up of the 62 species in the St. Andrews list together with the following 9 fungi not found at St. Andrews: *Bolbitius vitellinus*, *Corynetes arenarius*, *Geaster striatus* var. *minus*, *Inocybe bongardii*, *Lepiota cristata*, *Naucoria vervacti*, *Panaeolus foeniseccii*, *Peziza arenevaga* and *Psathyrella obtusata*.

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1. General view showing Cwm Rheidol mine where the polluted 'Red Stream' emerges from an adit.



2. Cwm Rheidol showing old mine adits emerging high on the wooded valley-side.

POLLUTION PROBLEMS OF THE RHEIDOL, CARDIGANSHIRE.

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Twenty-five years ago the Rheidol, which rises in a small corrie lake on Plynlymon, was a barren river heavily polluted by lead and zinc (James *et al.*, 1932). Today its waters support a considerable plant and animal population, the improvement culminating in the return of salmon to the river. In the years between, much research has taken place on various facets of the problems involved. Financial help has been difficult to obtain, but small sums have come from various sources, and the Departments of Chemistry, Botany and Zoology of the University College of Wales, Aberystwyth, have been greatly helped in their endeavours by sub-committees of the Standing Committee on Rivers Pollution of the Ministry of Agriculture and Fisheries. All the minutes and records were kept in the offices of the Ministry in Swansea and were destroyed when the building was blitzed in the Second World War. The Ministry then financed secretarial help and the complete record (5 volumes in all) was reconstituted by the present author from fragments collected from former members of the committees. Research has continued, spurred on by the pleasure of watching the recovery of the river. Recently the Rheidol hydro-electric scheme has brought the pollution problem into such new prominence that the time seems ripe for a fresh review of the position.

The rivers of the County of Cardiganshire run in a westerly direction to the sea, with the exception of the Teify, which takes a southerly course. They rise in the high plateau of the interior, which attains 2,468 feet at the summit of Plynlymon. The high plateau drops to a coastal belt which probably marks the position of an ancient coastline, and along this the rivers meander to the sea.

The mountains and hills of the interior are bare and provide only sheep walk, with coarse grass and heather, except where large areas have been planted successfully by the Forestry Commission. In places, the effects of planting have been very evident

in summer, when lines of trees, alternating with golden bands of *Ulex gallii* and purple *Erica cinerea* have beautified the mountain sides. Now that the trees are spreading a canopy, this colourful phase is unfortunately passing all too rapidly.

Woodlands clothe the valley sides, *Quercus petraea* being the dominant tree. The ground flora is not rich, though in the more remote spots, *Mecanopsis cambrica*, *Hymenophyllum tunbridgense*, *H. wilsoni* and *Trollius europaeus* still flourish. The coastal belt consists of good farm land.

Lead mines occur mostly in the high plateau, particularly along the valleys of the Rheidol and Ystwyth and their tributaries, though they also occur to some extent in the valleys of five other rivers. Dissection of the area by the rivers has been of great importance to the mining industry; they have provided water for driving machinery and for washing the ore, the valleys have given access to the interior of the county, and the depth of the dissection has enabled veins to be reached through adits in the valley sides instead of by sinking costly shafts. The valleys are broad "U" shaped areas, carved by ice and subsequently eroded so that tributary streams left at a much higher level now cascade from considerable heights to reach the floor of the main valley. Corrie lakes have been left among the hills, and these also have contributed a water supply for use in the mines.

The mines produced galena, generally with a trifling amount of silver, and in addition, some zinc blende and occasionally copper pyrites, iron pyrites and manganese. Adit levels provided ventilation and drainage. Steam engines were not used for drainage in Cardiganshire until the middle of the 19th century.

Though the mining industry is an ancient one, and records of the deleterious effects of the mine effluent date back to the eighteenth century, it was not until the nineteenth, when the Cornish method of crushing the ore was introduced, that harm to livestock and pollution of the rivers became serious. The great bulk of the ore was reduced by crushing to fine grains and powder which were washed in a tye. After treatment of the ore, the water which contained minute particles of lead was conducted through a series of slime pits where the velocity was checked and much of the sediment thrown down. Nevertheless the water itself subsequently carried much lead and zinc into the rivers,

and the old settling pits have remained through the years as a serious source of pollution, particularly when a high wind disseminates the dry material over the surrounding land. In addition, though mining has ceased for many years, mine detritus is carried down in quantity by flood waters, and this has been a further source of pollution. By the weathering of the surface of the old dumps and slime pits, galena and zinc blende are oxidised to soluble sulphates which are subsequently carried into the rivers by flood waters. The solubility of the sulphides is only 2.5 and 4.0 parts per 10 million respectively, but lead sulphate has a solubility of 315 parts per 10 million and zinc sulphate is readily soluble in water. After a period of drought zinc sulphate is often present on the surface of the tailings like icing sugar on a cake and this is all rapidly carried into the river in solution when the drought breaks. Unoxidised material is also carried down and deposited on the banks of the river, where it is exposed and oxidised when the water is low in time of drought, and it is then carried into the river in solution in the next flood. Polluted water flowing from the adits is an additional source of danger to the river. The lapse of time has been a partial remedy, but research results have enabled us to help the recovery of the Rheidol, to some small extent, and the degrees of toxicity of lead and zinc to plant life have also been ascertained. The experimental difficulties have been considerable, partly on account of the readiness with which lead salts precipitate in culture solutions and also because phosphate deficiency can easily arise and complicate the results.

The Rheidol is one of the swiftest rivers in Britain, having a flood velocity of 6 feet per sec. near the mouth. This, together with high acidity of the water, could be expected, in any case, to restrict the vegetation of the river. The presence of the old lead workings has, however, materially increased the barrenness of the river.

It was shown (Rees, 1937) that the microflora of the river was affected by the polluted effluent, and also by the mechanical grinding of the silt on the river bed. This is a matter of some significance because the microflora is an important stage in the food chain which had to be established if fish were to return to the river. The water in 1936 contained lead from 0.03-3 ppm. and zinc up to 36 ppm. in the worst places. It was shown by Jones

(1936) that the stickleback, which is sensitive to lead, was killed after 14 days in water containing 0.1 ppm. of lead, though trout had been caught in the river when it had that amount of pollution. When 3 ppm. of lead were present, insect species were the only surviving macrofauna, and the absence of case-bearing larvae was attributed to the absence of vegetable food.

The paucity of flowering plants in and near the river could be attributed partly to the toxicity of lead and zinc—Newton *et al.* (1936, 1938), Davies (1941), Newton and Glencross (1940)—and partly to phosphate deficiency, since the phosphate originally present in the soil combines readily with the lead and zinc and so becomes unavailable to the plants. It was found that different plants had different degrees of tolerance—see Hooper and Newton (1935), Hooper (1937), Newton *et al.* (1937), Davies (1941), Newton and Glencross (1940)—and that *Lemanea* and *Batrachospermum* were among the first colonisers in stretches of the river that were recovering (Carpenter, 1926). *Ranunculus aquatilis* was found to be one of the most sensitive plants to lead and zinc pollution: where it occurred in clean tributaries, it could be seen to stop abruptly where the tributary joined the polluted main river.

As the heavy metals from the surfaces of the dumps became leached out and pollution decreased, it was evident that some further experimental work might facilitate the establishment of vegetation either marginally in some of the old spoil dumps or in suitable places in the river where fish might ultimately find a favourable home. Observation showed that the Teify begins as a polluted river, but after it has meandered slowly through the long stretch of Tregaron Bog and breached the old moraine on the south side, it flows to the sea as a salmon river which the coracle-men fish. This demonstrated the value of peat as an absorbent for the soluble lead and zinc which emanated from the old Esgair Mwyn in the upper reaches of the river. Consequently, an experimental area bordering the Melindwr, a heavily polluted tributary of the Rheidol, was selected, and this was planted with young pines and other vegetation. Dressings of lime and phosphate were found to be beneficial, and it was hoped that a belt of deciduous plants might be established so that drainage from the polluted area might be cleaned before it entered the river. This has no doubt made some contribution to the recovery of the

river, but it is unlikely to be permanently efficacious in this particular location because the east winds blow the fine material from the old slime pits over the plants so that each pine tree becomes the centre of a miniature dune. However, the surface of the most of the spoil is now sufficiently well leached to minimise pollution, and this tributary will be unaffected by the new hydro-electric scheme.

When pollution decreased, the planting of vegetation in suitable places was undertaken (Jones, H., 1955a) and this was not only successful in itself, but it has led to taxonomic investigations (Jones, H., 1955b, c). It was found that *Glyceria fluitans* and *Callitriche intermedia* could be introduced successfully into water which has a summer depth of about 15 cms., an open situation unshaded by tree overhang, and a minimum current speed not more than 6 inches per second. The linear-leaved form will probably survive a current speed of 4 feet per second. After establishment of *Glyceria fluitans*, there is an increased growth in its shelter of both *Callitriche intermedia* and *Potamogeton polygonifolius*. Bryophytes also establish themselves in the river as it recovers, and *Scoparia undulata* and *Fontinalis antipyretica* occur in clumps. Doubtless, they would attain their maximum in a slower stream, but they have made a good headway in the Rheidol at a stage in the succession, though they would be unlikely to withstand the phanerogamic competition in parts of a slower river.

It should be mentioned that the rainfall on the high plateau is very considerable (average 91 inches per annum) and freak storms occur occasionally which bring down immense quantities of water into the river, which, together with much detritus, tend to scour away the existing phanerogams.

Concurrently with these botanical investigations, a zoological study of the Rheidol was made (Jones, J. R. E., 1950). The gut contents of the common insects have emphasised the importance of plants, both microscopic and macroscopic, in the food chain, and it is evident that the increased vegetation which has accompanied the gradual diminution of pollution has been paralleled in the increased fauna of the river.

By 1953 the river had so far recovered that the local angling society ventured to re-stock it, and salmon gradually began to return as far up as Cwm Rheidol. There were still one or two

danger spots, notably near the Ystumtuen mine, where a stream emerging from an old adit, very acid and heavily polluted with lead and zinc and carrying also iron oxide, cascaded into the river, though some of the water first seeped through a high dump of tailings. The volume of water into which this "red stream" flowed was the safety factor, and in consequence no serious pollution resulted, though tests showed that at times the small stream contained as much as 37.5 ppm. of zinc and 6.5 ppm. of lead.

In 1956 the new hydro-electric scheme on the Rheidol brought the problems of the pollution of the river sharply into focus again. It involved the establishment of large reservoirs in the upper reaches of the river, and the flooding of five old lead mines together with a very large area of old spoil heaps and mine detritus. In addition, the location of a dam in Cwm Rheidol would periodically reduce the flow of that part of the river which received the "red stream" and it was also proposed to blast certain rocks near the lower fall and create a fish-pass so that migratory fish could get up the river into the Cwm Rheidol valley where they had never before had access.

In order to convey water from the reservoirs to the power stations, tunnels have to be constructed, and one is extremely likely to cut through veins of ore as it emerges close to old workings on the valley side. Unless proper precautions are taken, this could provide a new source of galena and zinc blende which would gradually become oxidised, though, of course, the ores would not be crushed any more than was necessary for excavation.

The problems involved were obvious and numerous. Though pollution from most of the mines had been reduced to less than 1 ppm. of lead and 2 ppm. of zinc, there were still a few danger spots, the most notable of which was the "red stream" in Cwm Rheidol.

If pollution was to be avoided, a number of precautions were necessary and additional experimental work needed to be undertaken. For this the C.E.G.B. provided a research assistant (David Treharne) and we have also been privileged to have the co-operation and advice of Professor Briscoe of Imperial College, London.

A further series of culture experiments showed the high degree of toxicity of zinc sulphate to plants. . Though *Spirogyra* sp.

tolerated 12 ppm. zinc for 50 days, *Oedogonium* was killed by 2 ppm. zinc. Culms of *Phalaris* and seedlings of Red Fescue were both found to be seriously affected by the presence of zinc sulphate. They became yellow and made but poor growth, with a concentration as low as 5 ppm. of zinc.

It was evident therefore from this and all the earlier work that a means must be found of treating water contaminated by the sulphates of lead and zinc before they entered the river. Having regard to the natural cleansing of the Teify by the absorption of lead and zinc on to the surface of peat particles, and to the availability of hill peat in the area concerned, it was thought that peat treatment might be the solution to many of the problems which were likely to arise. Experimental work was undertaken in the laboratory and on the hillside. Contaminated water was passed at controlled speeds through beds of peat of various types, and it was found that, while the peat was effective in removing the lead, it absorbed zinc less well. Also, although peat could be used effectively on a laboratory scale, there were mechanical difficulties in conducting large volumes of water through peat beds of considerable thickness. Other means had therefore to be found of removing the contaminating sulphates.

Earlier visits to the Lake District and to the Mendips had shown that the effects of lead mine effluent were greatly reduced when the washing pits were on limestone. In the Lake District species of *Potamogeton* had been seen actually colonising old washing pits, and on the Mendips near Priddy, a large washing pit which is probably of great antiquity is colonised by *Phalaris*. In the Mendips the lead workings were in pockets in the Old Red Sandstone which forms the core of the anticline, but the washing pit is on the adjacent limestone of the flanks. These mines have been worked since Roman times, an old Roman road runs nearby, and it is interesting to speculate whether the site of the washing pit was determined by the configuration or by accessibility, or by some more subtle observation concerning the effects of acid and alkaline soils on the damage which the effluent caused.

Investigators have given different figures for different water samples and for different fish, but it is evident that the calcium ion concentration and the pH of the water are both important in modifying the effects of zinc and lead.

With this in mind and realising the impracticability of the large-scale use of peat in the many possible sources of pollution, attention was turned to the use of limestone, which can be obtained from a large quarry at Llandebie, south of the county. The limestone was crushed, and using material of a size $\frac{3}{8}$ inches to dust, the following experimental figures illustrate the results obtained:

<i>Polluted water</i>	<i>Lead.</i>	<i>Zinc.</i>
Untreated effluent	4.82 ppm.	19.00 ppm.
Treated with 1 lb. limestone per gallon	nil	1.58 ppm.
Treated with $\frac{1}{2}$ lb. limestone per gallon	0.04 ppm.	6.60 ppm.

The extraction is most complete when the limestone is most finely divided, and the rate of removal, though accelerated by agitation, is in any case very rapid.

These results provided the key to the solution of the problem and practical measures had to be taken to apply them both temporarily and permanently. It was evident that in the constructional work provision must be made for covering any ore that might be excavated with limestone chippings before oxidation could take place. Schemes had also to be devised whereby immediate filtration through beds of finely crushed limestone could be arranged if any quantity of polluted water from old workings was freed during constructional work.

Where the problem is permanent, as in the 'Red Stream' at Cwm Rheidol, the polluted water must be treated before it enters the river. Although three or four hundred thousand gallons of water a day may pour from two adits, high on the valley side, much of it seeps through the tailings so that only a very small quantity flows into the river. Nevertheless the water would be a serious menace to the reduced flow of the main river which will occur periodically at this point when the scheme is completed. The construction of a permanent plant is now in the hands of the engineers, a field experiment having shown that the addition of $1/20$ volume of lime water to the polluted water and its subsequent passage through a limestone filter bed completely eliminates metalliferous pollution.

In addition to the actual pollution problems of the river itself there are colonisation problems to be faced. Earlier results have shown that plants vary very much in their tolerance of the heavy

metals and the experimental areas on which the Forestry Commission have planted *Pinus sylvestris* on the Mendips illustrate the dangers of over-optimism. *Agrostis tenuis* seems to be the most tolerant of the grasses and *Thlaspi arvense* will clothe old workings even on Old Red Sandstone, but much remains to be done if the scars made by the hydro-electric scheme are not to add to those already created by the lead workings of earlier times. In the Compensation Reservoir in Cwm Rheidol there will be a considerable area between the river and the margin of the flood plain which will be alternately dry and submerged. This also will present a problem of colonisation. Fortunately the valley sides are wooded in most of the area concerned, so it may be possible by the selection of suitable trees to create a varied and colourful border to the reservoir which will merge upwards into the existing woodland of *Quercus petraea*, and so provide a solution to that part of the problem which is both practical and aesthetic.

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CAROLI LINNAEI PAN SUECICUS.

By JOHN RAMSBOTTOM
(British Museum, Natural History).

Time and again, over the years, the question of the authorship of the dissertations presided over by Linnaeus is raised.

There have been several accounts published in this country of the old method of examination at Uppsala, but none is wholly satisfactory. The course for a doctorate in medicine lasted from eight to ten years. It is not necessary here to go into details but only to make the point that, before publishing his thesis *pro gradu*, a candidate had already defended another (also printed at his own expense) called *dissertatio pro exercitio* because it was devised to test proficiency in writing and speaking Latin. The Professor usually supplied the material for this by lecturing, by dictation or by providing notes. The candidate (*respondens*) wrote the thesis in Latin; rarely he supplied the material himself. The examination was of the mediaeval kind, held in public with the Professor as *Praeses*, and with opponents to carry on the discussion in Latin, their task being made easier as they were provided with a printed copy of the thesis some days earlier. The system was altered in 1852 when new University regulations prescribed that the defender of a thesis must be its author.

Some of the confusion that has arisen is doubtless due to a failure to realise that 146 of the theses published are *pro exercitio*, only 40 being for doctorates; these latter are, naturally, usually concerned with medical subjects. Without a knowledge of the procedure, and the fact that the University regarded the *Praeses* as the author, there is plenty of evidence available that Linnaeus was justified in collecting the theses together and publishing them under his own name as *Amoenitates Academicae*. There are, first, categorical statements in notices Linnaeus wrote on some of the earlier theses in which he states that they are wholly his (e.g., *Betula* 1743; *Ficus* 1744). Next there is the internal evidence where facts are given that could have originated only with Linnaeus. Again there are statements by pupils (e.g., Solander, Acrel). Also among the miscellaneous manuscripts at the Linnaean Society of London there are odd notes and descriptions of species,

in Linnaeus's hand, which are obviously material used later in dissertations. Most important among them is a full draft for the thesis *Anthropomorpha*.* It is probable that in arranging and cataloguing the remaining manuscripts, Dr. A. Hj. Uggla will find further evidence of how Linnaeus collected notes for theses, for it should be realised that these provided a rapid and cheap way for him to publish.

In spite of all this, W. Rothmaler (in Fedde, Repert. Sp. Nov. XLIX (1940)) held that the theses as issued by the candidate "als geistige Produkte des Schülers zu bezeichnen".

One of the best known dissertations is *Pan Svecicus* which, because of its economic importance, was translated into Swedish, English and French. The title page reads:

DD

PAN SVECICUS**

quem

Consensu Ampliss. Facult. Med.

in Reg. Acad. Upsaliensi

Praesidi

viro celeberrimo et experientissimo

Dn. Dr. Carola Linnaeus

S:ae R:ae M:tis Archiatro

[etc.]

Publico examine modeste submittit

Nicolaus L: Hesselgren

Wermelandus

In Audit. Carol Major ad diem ix Decemb.

Anni MDCCXIX

H.A.M.C.***

Upsaliae

*T. Fredbarj. Menniskans cousiner [*Anthropomorpha*]. Vanda avhandlingar No. 21 (1956).

**The letters 'v' and 'u' were formerly interchangeable, 'v' being used at the beginning of a word.

***The thesis must have been reprinted almost immediately. The title page is as given in a separate large paper copy in Linnaeus's library: in a copy bound up with other dissertations this is given in full "Horis ante meridem consvetis". In the collection of theses published as *Amoenitates academicae* the title is given as *Pan svecus*.

This follows the accepted form and there is nothing to suggest that Linnaeus had a hand in it. He was to preside at an examination at a given place and time when Hesselgren was to defend *his* thesis in public.

No one reading the text carefully could imagine that it was the work of the candidate, yet there are various comments from "which Linnaeus claimed as his own" to that of E. G. Bobrov (*Dvuchsoletnie "Species Plantarum" Karla Linneja, 1753-1953, in Komarovskie Ctenija, VIII, 1954*) who holds that Hesselgren put in the binary names which convinced Linnaeus of the practicability of binomials; he believes that the trivial names appear in the margin in *Species Plantarum* because they were not inserted till the page proofs. This ingenious suggestion appealed to some as accounting for an innovation in typography.

There is a manuscript at the British Museum (Egerton MSS. 2039) which shows that Linnaeus was responsible for the subject matter of the thesis, that in it he evolved the binomial system of nomenclature and that Hesselgren evidently played a very minor part for his name is not in the list of the thirty who collected the data. It is given in B. H. Soulsby's *A Catalogue of the Works of Linnaeus* as "*Pan Suecicus* [MSS. of the Dissertation *Pan Suecus* . . .]". It is one of five items purchased in 1867 from C. M. Ridderbjelke, great-grandson of Linnaeus. Though well-known in one sense its importance seems to have been overlooked. There are several additional matters in the manuscript which are of interest but so far I have been able to find only one reference to it—A. Afzelius, *Egenhändig Anteckningar af Carl Linnaeus om Sig Sjelf* (1823) where, pp. 124-7, he describes *En. Anotations Bok för Åren, 1744-1750*.

Most of the introductory matter was copied by T. M. Fries and his note is in the University Library at Uppsala. It was published by A. Hj. Uggla as an appendix to a paper by Olof Svanberg, *Pan Svecicus, Ett Linneanskt Forskningsarbete av Aktuell Betydelse in Svenska Linné-Salskapets Årsskrift, XXXIX-XL (1956-7)*.

To assist the reader who cannot conveniently consult the original thesis, I think it useful to give the translation by B. Stillingfleet (*Miscellaneous Tracts relating to Natural History, pp. 184-201 (1759)*).

THE SWEDISH PAN.

By NICOLAS HASSELGREN

Upsal, 1749, Decem. 9.

Amænit. Academ. vol. 2:

§. 1.

The antients attributed the pastoral life to *Pan*, the care of flowers to *Flora*, hunting to *Diana*, and the cultivation of grain to *Ceres*. We, tho' acknowledging only one Deity, who governs all things, yet often use these names to denote the subject we undertake to treat upon. What word is now more known among botanists than the word *Flora*; by which they mean all those plants, which grow within a certain compass of ground; as our *Fauna Suecica* takes in all those animals, which are natives of Sweden? For a like reason we have entitled this small tract the *Swedish Pan*; intending thereby to denote the five domestic quadrupeds, which live upon plants growing in Sweden; or the devouring army of *Pan*, which lays waste the provinces of the *Swedish Flora*. We choose by this means to avoid a prolix definition, which is always disagreeable for the title of a book.

§. 2.

The pastoral life, by the testimony of both sacred and prophane history, is nearly as old as man himself; so that i would willingly derive the knowledge, which i am going to deliver, from the most ancient times. But altho' plants have been constantly obvious to the eyes of every man; yet i am obliged to declare, that we have nothing delivered down to us in any book concerning the kinds of plants proper for the different kinds of cattle; so that i may be sure of not disgusting my reader with stale matter new dressed up. For the whole of what i present to him is new.—Our illustrious president in his journey thro' Dalecarlia ann. 1734, made the first attempt this way, as may be seen *Flor. Lapp.* p. 158, where he says thus. 'In my journey thro' Dalecarlia, when we had climbed up the mountains, and were got into Norway, my fellow travellers being tired, and asleep, i wandered about in a dismal wood, and perceived that the horses easily distinguished wholesome from noxious food; for being very hungry, they devoured all sorts of plants, except the following: *meadow sweet*,

CAROLUS LINNAEUS

PAN
SVEVICUS

Sistens

ANIMA L. I. A, Phylivon

per

RESNUM ~~VERSTABKE~~

FLORAE SVEVICAE

inhospitata

videtur licet pinguescere sapra cicula
 barbagis pedundis, homini quod est acere venenum
 Linn. V. 897.

felices agricolae bona si sua norint

valerian, lilly of the valley, angelica, loose-strife, marsh-cinquefoil, cranes bill, hellebore, monks-hood, and many shrubs. This gave me a hint to recommend to the curious, that they would set about examining what plants such animals, as live on vegetables, viz. the *cow, the sheep, the goat, the deer, the horse, the hog, the monkey* and their species will not touch. An examination which would not be without its use, were 'it properly made'. Notwithstanding this recommendation no enquiry was made, till our president returned home from his travels thro' forreign countries, and made a progress thro' our own provinces. Afterwards professor Kalm, that worthy disciple of so great a master, followed his example; so that in his journey to Bahus we find mention made of some plants, which cattle either eat, or refuse. Ann. 1747 and 1748 our president undertook with great diligence not only to make experiments himself, but to excite his disciples, and auditors to do the same; of which number i was one. Thus at last many experiments were made, and repeated, especially by D. D. Hagstrom, Mag. E. G. Liidbeck, E. Ekelund, J. G. Wahlbom, L. Montin, F. Oldbers, J. C. Forskahl, A. Fornander, not to mention others, who strove, as it were, to out-do one another in finding the plants, which were suitable to different animals.

§. 3.

The difficulty however of examining all the Swedish plants, and getting animals proper for experiments, which ought all to be repeated, has hindered us from being able to give a compleat work on this subject. But the greatest part, and the most common vegetables of Sweden being now determined by us; what is wanting may be supplied from time to time. We hinted that animals proper for experiments, which ought to be taken from among *cows, goats, sheep, horses and swine*, are difficult to be found, for these reasons: first, because some plants are eaten by them in the spring, which they will not touch all the summer; when they are apt to grow rank in taste, and smell, and become stalky and hard. Thus many people eat the *nettle* in the spring; but who could bear it afterwards? Again, because some kinds of animals eat the flower, and will not eat the stalks; others eat the leaves and will not eat the stalks. N.B. When they eat the leaves, we say in general they eat the plant, otherwise there would be few grasses they could be said to eat. Œcon. Nat. Next, the animals

ought not to be over hungry, when we make our experiments, if we intend to make them properly. For they will greedily devour most kinds of plants at such a time, which they will absolutely refuse at another. Thus when they come immediately out of the house, they are not fit to make experiments upon; for then they are ravenous after every green thing that comes in their way. The best method is to make the experiments when their bellies are almost full, for they are hardly ever so intirely. Moreover the plants ought not to be handled by sweaty hands; some animals will refuse the most pleasing, and tasteful in that case. We ought to throw them on the ground, and if we find the animal refuses to eat them, we must mix them with others that we know they like; and if they still refuse them, we have a sure proof; especially if the same be tried with many individuals.

§. 4.

Our views do not extend beyond the Swedish plants, and that for the sake of our own œconomy. Let foreigners look to that part which concerns themselves, and thus our work will be confined within moderate bounds. We can produce above 2000 certain experiments, some of which were repeated ten times over, some twice as often. If we take the *Flora Suecia* Holm. 1745. and put to any herb the generical name, adding the number, and some epithet by way of difference, our work will be very much abridged.

§. 5.

It is manifest that the vegetable world was intended for the support of the animal world; insomuch that altho' not a few animals are carnivorous, yet these animals which they devour cannot subsist without vegetables. In this speculation we behold with admiration the wisdom of the Creator, which has made some vegetables absolutely disagreeable to some animals that live upon plants, while these plants are agreeable to others. And there are plants, which are poisonous to some animals, which are very wholesome to others, and on the contrary. This did not happen by chance, but was contrived for wise purposes. For if the Author of nature had made all plants equally grateful to all kinds of quadrupeds, it must necessarily have happened, that one species of them being remarkably increased, another species must have perished with hunger, before it could have got into better

pasture; the vegetables being consumed over a large tract of ground. But as it is ordained every species must by force leave certain plants to certain animals, so that they always find something to live upon, till they meet with better pasture; in the like manner we find it contrived in relation to the plants themselves, which do not all grow in the same countrey, and climate; but every plant has its place appointed by the Creator, in which it grows more abundantly, than any where else. From hence we may observe, that those animals, which chiefly live upon particular plants, chiefly abound in certain places. Thus the *lichen* or *liverwort*, Fl. 980. is found in greatest plenty on the cold alps, and therefore the *rhen deer*, which all winter live mostly upon this plant, are obliged to live there. The *festuca*, Fl. 94, which flourishes and spreads most on dry pastures, draws the sheep thither, which above all things delight in that kind of grass. The seeds of the *dwarf birch*, Fl. 777, which afford the best sort of food to the *rough-legg'd partridge*, and the *Norway rat*, Fn. 26. tempt them to dwell in these northern parts of the world. *Camels hay*, Mat. Med. 312. which above all plants, thrives on loose sand, draws the camel to choose those barren places, as they there find food most agreeable to them; not to mention many other similar instances. Trees, whose heads shoot up so high, that quadrupeds cannot easily reach them, afford nourishment for that reason to more numerous tribes of insects, as the *sallow*, the *oak*, the *pear*, &c. The Creator, who most wisely established this law, has as it were imprinted it on the organs of animals, that they might not offend against it thro' ignorance; and as every transgression has its punishment allotted, so also no offence against the law of nature can escape. Animals, which violate this law are punished by diseases or death; and hence we behold with admiration that brutes, which were designed to be guided by instinct, can by no means whatever be prevailed upon to act against it. If by chance it happens that any animal offends this way, and suffers for it, we vulgarly say it has taken poison; so that ignorant people wonder, not to say murmur at the wise disposition of the Creator, who has produced so many noxious plants; but without sufficient reason, for no one plant in the world is universally poisonous, but all things are good, as they came from the hands of the Creator. Physicians often mention that this or that plant is deadly, because its particles are of a nature apt to wound the

fibres of the body or corrupt the juices. But this is only respectively to the species of animals, e.g. the *sun-spurge*, Fl. 536. has a milky juice, which causes blotches in our skin and hurts our fibres, and therefore it is said to be poisonous; yet the *moth*, Fn. 825. almost entirely lives upon this plant, and prefers it both for taste and nourishment to all others, as it thrives best upon it. Thus one animal leaves that, which to itself is poisonous, to another animal, which feeds upon it deliciously. *Long-leaved water hemlock* will kill a *cow*, whereas the *goat* browses upon it greedily. *Monks-hood* kills a *goat*, but will not hurt a *horse*; and the *bitter almond* kills a *dog*, but is wholesome food for *man*. *Parsley* is deadly to small *birds*; while *swine* eat it safely; and *pepper* is mortal to *swine*, and wholesome to poultry. Thus every creature has its allotted portion. Animals distinguish the noxious from the salutary by smell and taste. Younger animals have these senses more acute, and therefore are more nice in distinguishing plants. An empty stomach will often drive animals to feed upon plants, that were not intended for them by nature. But whenever this has happened they become more cautious for the future, and acquire a certain kind of experience; e.g. the *monks-hood*, which grows near Fahluna, is generally left untouched by all the animals, that are accustomed to these places; but if foreign cattle are brought thither and meet with this vegetable, they venture to take too large a quantity of it and are killed. The cattle that have been reared in the plains of Schonen, and Westrogothia, commonly fall into a dysentery when they come into the woodland parts, because they feed upon some plants, which cattle used to those places have learned to avoid. In the spring, when the *water hemlock* is under water, so that the cows cannot smell it, they dye in heaps. But when the summer comes on and has dried the ground, they are very carefull not to touch it. It is also true, that all vegetables prohibited by nature to particular animals are not equally pernicious; and therefore though through necessity and hunger they eat them, yet they do not immediately dye; but it is certain that they cannot have from thence good and proper nourishment.

§. 6.

The end of this kind of knowledge is not bare curiosity, although were this the case every part of knowledge, which sets

forth the stupendous works of the Creator, is never to be looked upon as of no consequence. On the other hand we do not pretend to gain any medicinal advantages from these speculations, namely, to be able from hence to conclude, that this or that plant is noxious to man, because it is so to this or that brute animal. Nor do we for that reason approve of Wepser's experiments upon dogs, and other animals, as if any knowledge can be thence gained in regard to man. No, the end we aim at is merely oeconomic.

a. From these experiments we may know whether certain pastures afford good nourishment for this or that species of animals. We see, e.g. *heifers* waste away in enclosures, where the *meadow-sweet* grows in abundance, and covers the ground so that they can scarce make their way through it; the country people are amazed, and imagine that the pasture is too rich for them; not dreaming that the *meadow-sweet* affords them no nourishment. Whereas the *goat*, which is bleating on the other side of the hedge, is not suffered to go in, though he longs to be browsing upon this plant, which to him is a most delicate and nourishing food.

b. From these experiments we may almost be sure by affinity and analogy, whether meadows or pastures are salutary or noxious to particular animals; e.g. long experience has taught us that our *sheep* take up poison in marshy grounds, though no one till lately knew what was the particular poison. Yet the *spiderwort* 267. the *mouse-ear scorpion grass* 149. the *mercury* 823. the *sun-dew* 257, 8. the *hairy wood grass* 287. the *lesser spearwort* 458. the *butterwort* 21. have evidently suspicious marks. I will therefore propose a new experiment. The *andromeda* Fl. Virgin. 160. is known to be a most rank poison to sheep in Virginia. The *andromeda*, called by the people of New York *dwarf laurel*, Cold. Act. Upsal. 1743. p. 123. is very fatal to the sheep in New York. These two plants are of a different species, but of the same natural genus, and therefore have the same vertues. Amongst us, especially in the northern parts, the wild *rosemary*, *andromeda* 335. grows every where in marshy grounds, which being of the same natural genus with the foregoing, we may reasonably conclude that it destroys our sheep. To this we may add, that it is on account of three other species of *andromeda* 336, 7, 8. which grow on the Lapland mountains, that the sheep

there never are healthy; and lastly although the *cistus ledon* 341. is not a species of *andromeda*, yet being of the same natural class, it is not unlikely but that this plant is far from affording good nourishment to sheep. This conjecture gives our shepherds an unexpected opportunity of making experiments with their sheep; and indeed they cannot omit to do it without being justly blameable, since on this the health of their whole flock depends. It is particularly to be noted upon this occasion, that the botany of America, a countrey so far disjoined from us, gives a hint for considering things of the greatest use, of which the antients did not so much as dream.

c. From hence the œconomist may truly judge of his meadows, and know that some are vastly preferable to others for certain animals. For although cattle, pressed by necessity and hunger, will feed upon vegetables less gratefull to them; yet it is not to be doubted but that they are not equally well nourished by these as by others. Thus the Dalecarlians are obliged in a scarcity of wheat to support themselves by *bread* made of the *bark* of the *pine*; yet it does by no means follow from hence that this affords proper nourishment. We see that *horses* in time of war, when pressed by extreme hunger, will eat *dead hedges*, but we cannot hence conclude, that wood is good food for them.

d. The industrious farmer may judge from hence, when he sows his meadows with hay seeds for pasture, that it is not indifferent what kinds of seeds he chooses, as the vulgar think. For some are fit for *horses*, others for *cows*, &c. *Horses* are nicer in choosing than any of our cattle; *siliquose* and *siliculose* plants particularly are not relished by them. *Goats* feed upon a greater variety of plants than any other cattle, but then they chiefly hunt after the extremities and flowers. *Sheep* on the contrary pass by the flowers and eat the leaves. Not to mention the different disposition in different animals as to grazing near the ground or not. The countreyman who understands these things, and knows how in consequence to dispose of his grounds, and assign each kind of cattle to its properest food, must necessarily have them more healthy and fat than he who is destitute of these principles. The good œconomist will observe the same of his hay. For although many herbs, when dry, are eat, which when green would be refused, it does not follow from hence that they yield good nourishment. Much might be added concerning the propension

of cattle to this or that plant, which the compass of this small tract will not admit of; e.g. that *sheep* above all things delight in the *festuca* 95. and grow fatter upon it than any other kind of grass; that *goats* prefer certain plants, but being led by an instinct peculiar to themselves, they search more after variety, and do not long willingly stick to any one kind of food whatever; that *geese* are particularly fond of the feeds of the *festuca*, Fl. 90, that *swine* greedily hunt after the roots of the *bull-rush* 40. while they are fresh, but will not touch them when dry. Hence it appears that it is in vain to contrive engines to extract the roots of the *bull-rush* out of the water, and dry them for the use of these animals in winter. Because these animals spoil the meadows where the *scorzonera* grows, in order to come at its root, which they delight in; and also the fields, to get at the roots of *clowns-all-heal*, the husbandman imagines they do good to his fields by ploughing the ground and eating the roots of *couch-grass*, whereas they never touch them, but when pressed by the utmost necessity.

§. 7.

To give a view of my design in a few words, I have disposed the plants mentioned in the Flora Suecica according to their numbers; and to be as short as possible, it was necessary to add the generical name with a short and incomplete epithet, which however may be illustrated out of the Flora itself. I have distinguished the cattle against every plant into five columns. The first of which contains *oxen*. The second *goats*. The third *sheep*. The fourth *horses*. The fifth *swine*. By the mark (i) i have denoted those plants which are eaten; by the mark (o) those which are not eaten; by both together those which are sometimes eaten, sometimes refused; or are eaten when cattle are more used to them, and are more hungry, otherwise not.

§. 8.

Upon the first view of this subject the reader will perceive, that it is not treated completely, so that every Swedish plant is pointed out, and by what animals it is eaten. What generally happens upon breaking up old pasture lands, viz. that for the first years it cannot be cleansed from all useful weeds, and be laid down fine like a garden, but will here and there have rough tumps and hard clods, unless we will let it lye fallow for a very long

time; the same or something like it has happened upon this occasion.

I am apt to believe however that the reader will be better pleased that I have opened this new scene, than if I had waited longer in order to gain farther light. For since there are many people here curious in botany and œconomy, i hope they will all lend a helping hand, that i may one day be enabled to give a more compleat edition of this piece.

Thus far we have given 2314 experiments. From these it appears that

Oxen	eat	276	refuse	218	plants
Goats	„	449	„	126	„
Sheep	„	387	„	141	„
Horses	„	262	„	212	„
Swine	„	72	„	171	„

And thus these animals leave untouched 886 plants.

These animals will not eat any kind of *moss*.

The goats are very fond of the *algae*.

Some of them greedily devour the *fungi*, others will not taste them. But we recommend farther trials in relation to these matters.

Then follows an account of some trials made by Dr. O. Hagstrom to the same purpose in relation to *rhen deer*, but as they no ways concern us, i have omitted to mention them.

* * *

In the following discussion, thesis refers to the published dissertation, manuscript to Linnaeus's (unpublished) draft.

The title page (Plate I) does not mention Hesselgren—it is “Caroli Linnaei Pan Svecicus”. The quotation from Lucretius is significant, for it appears at the end of the thesis. The introduction is really a series of notes, much shorter and less complete than the thesis but containing additional facts (Plate 2). It is in Swedish with an occasional break into Latin as is frequent in Linnaeus's notes.

Miss Agnes Traviss of Stockholm kindly made a translation of the part already published: the remainder was apparently not copied by T. M. Fries. These somewhat disjointed jottings I had photographed and took to Uppsala where Dr. A. Hj. Uggla deciphered and translated them with the amazing ease for which he is noted. To both these friends I express my warm thanks.

Skaparens väja, som på vårt förtal ligga of
alltså för igenom med en uttöfelig vilhet
inrättade, de vi som här fram en ny vilka-
skap hem intill denna dag giemt sig undan.
men är dock så tillräckligt, att den till sin
höga föddan många till älsk och män.
Det är klart att världen med alla sine öter
är inrättad till föda för djur-riket, så att
djuren ej må ha någon öfverflöd utom kripa
an växter utom jord.

Da vi dotta betrakta finne vi med förundran
kun en mild Skapare ibland växtriket lagt
en ganska stor öter, som del är ofsmaka-
lige för vår förund och del är delvis giftige
och dodelige.

Men da vi gå vidare omkring märka vi af-
ven två de somaste giften, den nyttigaste
Skaparens inrättning. Skaparen har gifvit
kvarn flög djur sin mest giftige öter
örter, deremot förbudt andra för andra
så att icke välk för äter, men icke allt
af alla.

Skaparen lagar i naturen vår alltid så ställe
att de ofviges budare genom ofvare budellena
få sitt förtänte straf. Lagen har Skaparen
sat på alla djurs hänger att nägor, att in-
till men inrättade genom tillen oförvänder
Cim Skenket talog hem intill, för att ofvänder
da för djur-riket. Lär om nerverne bare
laga, som det luktas och smakar, så öger
det att förmå i kroppen blömt.

Om en nödig Skapare ej varit denna lag, utan
låt att vara kienligt och hälspänd för
alla, hade skedd att om att flöte förvit
sig, att förmå, och gr. Subnen, och slutade
upått att på hola 20 milerna, hade kon-
fö, geller och dode of hungen da de kom-
mit på samma ställe, som nu finna
för sig något quaspaende, att munglone att
de kunna berya lifvet till de de kenne
i kienligare del.

“The works of the Creator, which on our globe lie everywhere open to our eyes and are arranged with incredible wisdom, show here a new science which, until this day, has been hidden but is, nevertheless, so extensive that it will need a hundred years—and man—to get its real height.

It is clear that the realm of botany, with all its herbs, is contrived to feed the animal world, so that animals can no more exist without plants than plants without soil.

In considering this we find with surprise how a mild Creator has put in the vegetable kingdom quite a large number of herbs that are, partly, distasteful to our cattle and, partly, completely poisonous and deadly.

However, in travelling about more widely, we notice also in the strongest poisons the most useful device of the Creator. The Creator has given every kind of animal its food and its special herbs, whereas He has forbidden some for others, so that, in the end, everything may be eaten, but not everything by all.

The laws of the Creator in nature have been thus laid down that the transgressor through the transgression receives his deserved punishment. The law has been imprinted by the Creator on all animals' tongues and noses so that nothing can pass undetected through the customs barrier. (Nothing is said here about minerals, for they would be absurd as food for animals). Here the nerves are bare; the way it smells and tastes, so it acts and after that is digested in the body.

If a gracious Creator had not made this law but let everything be suitable and healthy for all, it would have happened that if a generation had increased too much, for instance swine, and thus eaten up everything within a range of 20 [Swedish] miles, cows, sheep and goats would have died of hunger when arriving at the same fields, whereas now they find at least something left standing for them so that they are able to save their lives until they reach more suitable pastures.

Thus, one animal leaves its poison in order that others may eat their food, e.g.

Water Dropwort is forbidden to the horse, but relished by the cow.

Water Hemlock is forbidden to the cow, but relished by the goat.

Pepper is forbidden to the pig, but relished by the hen.

Monkshood is forbidden to the goat, but relished by the horse. Parsley is forbidden to the sparrow, but relished by the pig. Bitter Almond is forbidden to the dog, but relished by man.

Medical men believe, generally, that man's food consists solely of plants that have smooth particles; on the other hand those with sharp ones are downright poisonous. This, however, is otherwise, e.g.

Euphorbia 436 [*E. helioscopia*] has milk that corrodes our flesh, just as spirits of nitre corrodes iron, and, consequently this plant is eaten by few animals or none. *Phalaena* 825 is a moth living entirely on this herb; were it able to speak, it would probably say that none had milder, smoother and sweeter particles in itself than this. *Sic de caeteris*.

Trees lifting up their crowns so that animals do not reach them, have more kinds of insect quartered on them than have other plants; this may be seen in willow, oak, poplar, apple, by means of which Passeres and small birds get their food out of the trees where, to our eyes they are only making music.

All animals sense what is good for them through smell or taste but a hungry stomach often lets that be introduced into the stomach which has not been so precisely indicated by the customs barrier, and the animals, therefore, often must pay the penalty according to the code of punishment against God's law; e.g. when cows come to Kinnekulle or Billingen for sale and land there in meadows full of plant 823 [*Mercurialis perennis*] they immediately fall into a dysentery, and often die; but after that they never get this disease, indicating that they swallowed some herb that was not theirs, which earlier they did not know very well, but since have been on their guard against.

When cows which have been bought are turned out to grass in the meadow at Stemshögen at Fahlun, one may be sure that they will become sick or die by coming upon Monkshood 442 [*Aconitum septentrionale*], but the accustomed cows know from dear experience to beware of it.

The usefulness of this knowledge is so great that I dare to call it the basis of all shepherds' life and *Oeconomia pecuaria*.

He who is acquainted with plants and knows which plants are eaten or not eaten by various animals may be able to judge at once whether it gives good or bad grazing for beast, sheep,

goats, horses or pigs and to organize his breeding and grazing accordingly, e.g. a meadow or field with plenty of

1. *Ledum*, *Andromeda*, *Anthericum*, *Myosotis*, *Pinguicula*, *Drosera*, *Mercurialis*, *Equisetum*, I judge harmful for sheep.
2. With plenty of *Cicuta* [*virosa*] is not for beasts.
3. With plenty of *Phellandrium* [*Oenanthe aquatica*] is not for horses.
4. With plenty of *Festuca* 95 [*ovina*]; delicious for sheep.
5. With plenty of *Ulmaria* [*Filipendula ulmaria*], *Ranunculus* [*acris*]; not for beasts.
6. With plenty of *Melampyrum*; delicious for beasts.

Some plants are not eaten until they have become frost-bitten like *Asclepias* [*Cynanchum vincetoxicum*], some are eaten only when they are young, some are eaten only by a hungry stomach, some by custom *et necessari[tate]*.

EXPERIENTIA.

Caltha is not eaten at all by cows. Therefore those who have said that *Caltha* makes butter yellow are wrong.

Melampyrum on the other hand is the best for cows and to get yellow butter. *Fl. lapp.*

Festuca 95 is the best fodder of all for sheep. It is so good that they at last die from fatness where there is very much of this grass, and they refuse all other sorts of fodder. *Fl. goth.*

The hen would prefer to die rather than eat lupin.

Parrots eat the seeds of *Carthamus* without harm.

Quails eat *Helleborus* without harm.

Starlings eat *Cicuta* without harm.

Petroselinum kills sparrows and geese.

Andromeda affinis.

The occasion for this observation I got in 1734 when I came over the Dalecarian mountains to their western side where the horses were tethered in the richest pasture but left many plants untouched. *Fl. lapp.*

- 1 The plants I have listed according to *Flora suecica*.
2. The number in the left margin is the same as in the Flora.
3. Who wants to know some synonyms may open the floras.
4. I have listed no other plants than the Swedish ones.
5. To the right are five columns of which No. (1) means cows, (2) goats, (3) sheep, (4) horses, (5) pigs.
6. The symbols in these five columns are either 1 or 0.
7. Here 1 means that the plant is eaten by the animal.
0 means that the plant is not eaten by the animal.
- 9 When 01 means that the plant is not eaten fresh, but when dried.
§ means that the plant is sometimes eaten but sparingly, mostly it is passed over by the animal.
† means that the plant is surely a poison and deadly.
10 means that the plant is eaten fresh, but not dried.
11 means that the plant is eaten with the greatest pleasure".

The published tables do not use the symbols § and †. Also they end with species No. 856 whereas the manuscript continues the numbers to 1140, i.e. all those given in *Flora suecica*, though there are few names and little additional information. As will be seen from Plate 3, the manuscript list also differs in giving no epithet for monotypic genera; also it is not divided into Monandria, Diandria, Triandria and so on except by double lines across the column. There are other differences in detail.

Sections 4 and 7 of the thesis give the reason for the adoption of the specific epithet or, in other words, the binary or binomial system of nomenclature. The first published use of this was in the index to Linnaeus's travel book *Öländska och Gothlandska Resa* in 1745: the second in the thesis *Gemmae arborum* (resp. P Löfving) 1749—a month before *Pan Svecicus*. Löfving was one of those specially mentioned by Linnaeus among the thirty helpers in obtaining data (he specialised on the food of goats): his was one of the few dissertations where the candidate himself must be given credit for its contents. His work, however, had to be approved by Linnaeus; the use of binomials was obviously nothing more than the adoption of a method already established.

		Potentilla	Cypripedium	Oribancha	Lychnis	Smilax
1.	Salicornia	0		0	0	1
2.	Hippuris	0	1	0	0	0
3.	Callitriche					
4.	Ligustrum	1	1	1	0	
5.	Cerata			1		
6.	Veronica tenuifolia	1	1	1	0	0
7.	spicata	1	0	1	0	
8.	major		1	1	1	
9.	reticulata			1	1	
10.	oblongifolia	1	1		1	0
11.	rotundifolia	1	1	0	1	0
12.	Hebecladus madag.			1		0
13.	alpina					
14.	femina		1			
15.	linifolia					
16.	caulic. adhaerent.					
17.	oblong. caulicul.					
18.	subulosa					
19.	vulgaris					
20.	triphyllor minim					
21.	Pinguicula vulgaris			1		
22.	alba					
23.	lapponica					
24.	Utricularia major					
25.	minor					
26.	Verbena			1		
27.	Zycopus	0	1	1	0	
28.	Salvia Horminum.	0	1	1	0	
29.	Anthoxanthum	1	1	1	1	
30.	Valeriana vulgaris	0	1	1	1	0
31.	— Diaca			1		
32.	— Locusta		1	1	1	0
33.	Aris		1	1	1	0
34.	Schoenus vulgaris		1	1	1	0
35.	— monsp.					
36.	— nigricans					
37.	— minimus					
38.	Scirpus filicatus	1	1	1	1	0
39.	— montan.		1	0	1	1
40.	— lacustris	0	1	0	1	1
41.	— palustris		1			
42.	— sp.					

Linnaeus gives no hint of why he used specific epithets in the index of 1745. I cannot subscribe to the idea that the binomial system, which has proved invaluable in biological science, had its origin as an indexer's paper-saving device. It was not Linnaeus's way to make any innovation without some explanation and the assumption must be that he was already using the method. The clue seems to be in the manuscript. There is, however, the difficulty of dates. In Section 2 of the thesis is the statement that the work began in 1747 (i.e. two years after the index), but this can refer only to the organized teamwork. Linnaeus had long been interested in the food of animals and, indeed, P. Kalm had sent him a list of such plants from Bohus-Län in 1742. So far, however, I have not found convincing proof that the manuscript was started before the publication of the index. Meanwhile it may be pointed out that the binomials of monotypic genera given in the index—*Salicornia herbacea*, *Lycopsis vulgaris*, *Iris palustris*, etc.—are absent from the manuscript suggesting that the index was later. Further, the names of mosses in the manuscript have their *Flora suecica* names to which afterwards an epithet has been added.

THE CONSERVATION OF THE SCOTTISH FLORA.

By J. GRANT ROGER

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INTRODUCTION.

In Scotland, as in most other countries, efforts towards the conservation of representative types of natural vegetation have been developed effectively only within recent years. As a rule in the past our native plants, as species or as communities, have been exploited whenever they or their habitats have been required for man's use, with little or no concern for their ecological, aesthetic or educational values. Nevertheless there is evidence from many carvings in stone and references in literature that our native flora was carefully observed and appreciated for its beauty from mediaeval times onwards. Laws for the conservation of forests were indeed introduced in the twelfth century, but the "forests" referred to included treeless tracts and such legislation seems to have been largely for the benefit of animals of the chase. Later, from the early fifteenth century, laws passed by the Scottish Parliament were primarily concerned with the preservation of timber and the planting of trees to ensure a supply of timber. However, the depletion of large areas of woodland went on steadily in spite of the Acts of Parliament and it seems that over the more populous lowlands generally there was a great scarcity of timber even in the fifteenth century, and this scarcity became inevitably more acute with the increase in population and the advancement of agriculture.

Many factors contributed to the depletion of the native woods such as natural outbreaks of fire, gales, felling for fuel and building, their devastation in war time, and their destruction as refuges of wolves and thieves. Extensive woods in several parts of the country were ruthlessly exploited as a source of fuel for iron-smelting, notably in Wester Ross, Moray and Cowal. Yet there were up to the close of the eighteenth century large areas of natural woodland surviving in Scotland, especially in the remoter parts of the Highlands, and, from about the middle of the eighteenth century onwards, there was considerable planting of trees by enterprising proprietors, as at Glamis, in Angus. Even

in the early part of the previous century there was a nursery at Edzell Castle, referred to by Cox (1935), where among the trees reared were birch, holly, fir (Scots pine), and elm.

The destruction of woodland was especially severe during the early nineteenth century, chiefly for the purpose of extending sheep pasture; indeed both in the Highlands and in the Lowlands much of the pasturage for sheep replaced natural forest land. In many areas goats, deer and rabbits greatly hindered the regeneration of tree species. Thus the native woods, which in early mediaeval times covered probably a third or more of the total area of Scotland, were reduced to their present area of about one-twentieth of that of the whole country.

But besides the woodlands most other types of vegetation were steadily depleted by man's activities. For instance, the plant communities of great areas of bogland and of many lochs were eliminated by draining operations and much of the natural montane vegetation suffered by drastic burning of moorlands and excessive grazing pressure. The history of man's influence on the native vegetation of Scotland with its associated animals has been most thoroughly recorded by Ritchie (1920).

Although the depletion of our native vegetation proceeded steadily with increasing land utilisation there developed gradually a scientific interest in the flora, 'this interest being greatly stimulated by contact with the work of Ray and the great botanists of the Continent. Botanical activities in Scotland, formerly pursued by very few individuals, became strikingly evident from the middle of the nineteenth century. The Universities, especially Edinburgh University with its associated Botanic Garden, were the centres of early work in field botany, and indeed the vigorous encouragement and example set by Scottish teachers of botany stimulated hundreds of students to study more closely wild plants in relation to their habitats. Scientific societies, too, were responsible for much botanical activity resulting in a steady stream of publications relating to the Scottish flora. Most prominent in this respect have been the Botanical Society of Edinburgh (founded in 1836), the Natural History Society of Glasgow (founded in 1851, and now represented by the Andersonian Naturalists of Glasgow), and the Perthshire Society of Natural Science (founded 1867).

Towards the close of the nineteenth century and in the early part of the present century a strong ecological approach in studies of the Scottish flora was developed and particularly exemplified in the work of R. Smith (1898, 1900 and 1903), W. G. Smith (1905 and 1911) and Matthews (1914), while Tansley's *Types of British Vegetation* (1911) became the invaluable handbook for all contemporary students of British plant ecology.

PROGRESS TOWARDS ORGANISED CONSERVATION.

Great support was given to the cause of nature conservation in Britain by the formation and activities of the Society for the Promotion of Nature Reserves (founded in 1912 and incorporated by Royal Charter in 1916). Indeed very much of the preliminary work required as a foundation for nationally-organised conservation was due to the initiative and persistent enthusiasm of the Society. Then, in *Our Heritage of Wild Nature* (1945) Tansley very clearly emphasised the need for conserving adequate samples of our wild and semi-wild vegetation; firstly, because these were integral parts of the natural landscapes which formed much of the background of our national life; secondly, because they were essential for the ecological work, with its potential particular applications; and, thirdly (but not least important) because of their essential value in the teaching of natural science and for education in the widest sense.

In 1946 the Scottish Wild Life Conservation Committee was appointed by the Government to consider and advise the Scottish National Parks Committee as to the steps which it would be desirable to take to conserve wild life in Scotland, and it prepared two reports, published by the Department of Health for Scotland (1947 and 1949). A Committee with similar functions for England and Wales—the Wild Life Conservation Special Committee—had been appointed in 1945, and its report was published in 1947. The recommendations of both Wild Life Committees were accepted in principle by the Government and, on 29th March, 1949, The Nature Conservancy was constituted by Royal Charter as a body responsible to the Privy Council's Committee for Agricultural Research and Nature Conservation, (1) to provide scientific advice on the conservation and control of the natural flora and fauna of Great Britain, (2) to establish, maintain and manage Nature Reserves in Great Britain including the

maintenance of physical features of scientific interest, and (3) to organise and develop the research and scientific services related thereto. In order to further the objects of the Charter in Scotland the Conservancy's Scottish Committee was formed and Professor J. R. Matthews, a member of the Conservancy, was appointed Chairman of this Committee. Then, to give additional support to the work required of The Nature Conservancy, Sections relating to Conservation were included in the National Parks and Access to the Countryside Act of 1949. For instance, Section 16 of this Act enables the Conservancy to enter into agreements with owners and occupiers whereby land not actually acquired for the purpose may yet be managed as a Nature Reserve. Again, Section 21 of the Act enables local planning authorities, in consultation with the Conservancy, to establish and manage Nature Reserves within their areas, while Section 23 places a duty upon the Conservancy to notify to the local planning authority any areas of land of special scientific interest.

NATURE RESERVES.

All the Reserves selected for mention below (because of their botanical importance) include areas, or parts of areas, recommended for conservation by the Scottish Wild Life Conservation Committee (1949), except Rassal, Glen Diomhan, Inchnadamph, Tynron and Clairinsh, which were considered to be of Reserve status, following investigations carried out by the Nature Conservancy. There is freedom of access of all the Nature Reserves referred to, except Inchnadamph, most of Rhum, part of Caerlavrock and, in autumn, parts of the Cairngorms. The collecting of specimens on Nature Reserves is not, of course, permitted, unless for definitely authorised scientific purposes.

Ben Lawers, Perthshire.

In 1950, the National Trust for Scotland (founded 1931) purchased some 8,000 acres of land on Ben Lawers and Beinn Glas, overlooking Loch Tay, chiefly in order to safeguard the exceptionally interesting and beautiful mountain flora of that area. Within the Trust's property, as is well-known, there are indeed a number of the rarest flowering plants in the British Flora, e.g. *Draba rupestris*,* *Erigeron borealis*, *Gentiana nivalis*,

*Nomenclature used throughout follows Clapham, Tutin and Warburg (1952).

Minuartia rubella, *Myosotis alpestris*, *Saxifraga cernua*, *Sagina intermedia* and *Veronica fruticans*. Attractive notices have been placed at vantage points on the mountain slopes requesting visitors to refrain from collecting specimens, and a booklet *Ben Lawers and its Alpine Flowers* has been published by The National Trust (1955).

Beinn Eighe Nature Reserve, Wester Ross.

This area of 10,450 acres was declared a Nature Reserve by the Conservancy in November, 1951, and was the first National Nature Reserve to be established in Great Britain. The primary object of the acquisition was the preservation of the very interesting native Scots pine woodland, Coille na Glas Leitire, referred to by Tansley (1939) and situated on the lower slopes of Meall a' Ghiubhais, overlooking Loch Maree. Apart from this woodland, however, the Reserve, which ranges in altitude from about 40 feet at Loch Maree to 3,188 feet on Sgur Ban of Beinn Eighe, includes several plant associations of considerable interest, notably the dwarf shrub heaths and moss heaths described by Poore and McVean (1957) and the communities dependent on the outcrops of serpulitic grit. An account of the flora of the Reserve has been published by Ribbons (1954).

Directly associated with the Nature Reserve is the Anancaun Field Station, adjoining the Reserve Warden's house, where there are hostel and simple laboratory facilities. Botanical research in progress at Beinn Eighe, based on Anancaun, is chiefly in aid of the rehabilitation of the Scots pine woodland and montane plant communities. The ecological conditions in Coille na Glas Leitire can be very usefully contrasted with those prevailing in the Scots pine woods of the Eastern Grampians, particularly those of the Cairngorms Nature Reserve.

Aberlady Bay Local Nature Reserve, East Lothian.

This, the first Local Nature Reserve to be set up in Scotland under Section 19 of the National Parks and Access to the Countryside Act, 1949, was established by the East Lothian County Council in 1952. It includes 1439 acres of foreshore, salt-marsh and dunes and is of importance mainly because of its botanical and ornithological interests. Records of the vascular plants found in the area are given in *The Field-Club Flora of the Lothians* (Martin, 1934).

The following areas are all, like Beinn Eighe, among the National Nature Reserves established by the Nature Conservancy. (A few of the Conservancy's Reserves are not treated here because they have comparatively little botanical importance.)

Tentsmuir Point Nature Reserve, Fife.

This area of 92 acres at the mouth of the Tay was purchased from the Forestry Commission and declared a Nature Reserve in 1954, primarily for physiographical and ecological studies because of the remarkable rapidity with which the land here is accreting. The Reserve, which includes a very broad sandy inter-tidal zone backed by dunes and slacks, has a rich flora, with several species that are rare or very local along the east coast of Scotland, e.g. *Carex maritima*, *Centaureum littorale*, *Dianthus deltoides* and *Teesdalia nudicaulis*.

Cairngorms Nature Reserve, Aberdeenshire and Inverness-shire.

The Cairngorms Reserve, declared in 1954, covers 39,689 acres between Upper Deeside and Speyside and is by far the largest Nature Reserve in Britain. It consists of the following contiguous areas: (1) 17,500 acres on the estate of Mar; (2) 14,570 acres on Rothiemurchus; (3) 2,290 acres on Inshriach; and (4) 5,329 acres on Invereshie. The first three areas are Nature Reserves by Agreements with the Estates mentioned, while the fourth, on Invereshie, was purchased by the Nature Conservancy, and is thus entirely under the Conservancy's control.

The chief aim in establishing this great Reserve was to safeguard its woodlands and mountain habitats, with their associated plants and animals, so that these might persist and develop naturally with a minimum of interference from man's activities, but controlled to some extent by scientific management. Within the Reserve, which ranges in altitude from 840 ft. to 4,296 ft. are some of the largest and finest natural woods of Scots pine (*Pinus sylvestris* ssp. *scotica*) surviving in the Highlands, while above the woodlands the plant communities of the mountain sides, corries and severely exposed summits are of great ecological interest. Over 200 species of vascular plants occur on the Reserve and among these are some of the rarest members of the British Flora, such as *Carex lachenalii*, *Cerastium cerastoides*, *Luzula arcuata*, *Poa flexuosa* and *Saxifraga rivularis*.

Watt and Jones (1948) have given the best general account of the plant ecology of the Cairngorms, while Metcalfe (1948), Burges (1951) and Ingram (1958) have dealt in detail with the vegetation of the moors, higher slopes and summits. An account of the distribution and status of the flowering plants of the region has been given by Roger (1956).

There is freedom of access on the Reserve at all times except (1) in Glen Derry, Mar, during the stalking season, between 15th August and 15th October, and (2) in the Glen Geusachan Deer Sanctuary, Mar, between 15th August and 30th November.

Isle of May Nature Reserve, Fife.

The Isle of May (140 acres), in the Firth of Forth, became a Nature Reserve in 1956 by an Agreement with the owners, the Commissioners of Northern Lighthouses. The Reserve is primarily valued as a centre for ornithological observations but it has a very interesting flora which has been recorded in detail by Eggeling (1956), while the bryophyte flora is discussed by Watson (1957).

Rassal Ashwood Nature Reserve, Wester Ross.

This Reserve, established by an Agreement with the proprietor, occupies 202 acres on Durness Limestone, about three miles north of Loch Kishorn, and includes as its chief feature the most northerly ashwood in Britain. The interesting and beautiful flora of this remarkable woodland, with its hummocks of moss-covered limestone, has now been protected by fencing against grazing animals. The limestone plant communities beyond the area of the ashwood are also of interest.

Silver Flowe Nature Reserve, Kirkcudbrightshire.

Here within an area of 472 acres leased as a Reserve in 1956, is a remarkable series of largely undisturbed bogs of great ecological importance. There are seven bogs in the series, ranging from a convex raised bog, at the lowest elevation, to a "blanket" bog at the highest level, and over the bogland generally are numerous "hummock-pools". Very thorough ecological studies of the Silver Flowe have just been published by Ratcliffe and Walker (1958).

Glen Diomhan Nature Reserve, Isle of Arran, Buteshire.

This small Reserve (24 acres) was declared in 1956, under an Agreement with the owner, for the protection of the two rare endemic species of whitebeam, *Sorbus arranensis* and *S. pseudo-fennica*, which are well represented in the glen. These very interesting shrubs formed the subject of a paper by Landsborough (1900).

Inchnadamph Nature Reserve, Sutherland.

The Inchnadamph Reserve was established by an Agreement with the owner in 1956. It covers an area of 3,200 acres south-east of Loch Assynt, long known to botanists because of the very interesting flora on its limestone rocks. Of special ecological interest are the limestone pavement areas covered by willows, chiefly *Salix myrsinites*, and described by Poore and McVean (1957). An account of the rarer vascular plants occurring in the area has been given by Raven and Walters (1954).

St. Kilda Nature Reserve, Inverness-shire.

The famous St. Kilda group of islands (2,107 acres in all) was leased from the National Trust for Scotland and declared a Nature Reserve in 1957, principally because of its great zoological interests. However its flora too is of scientific importance, largely because of the extreme westerly position of the islands—45 miles beyond the Outer Hebrides. A very useful paper on the vegetation of St. Kilda has been published by Poore and Robertson (1949).

Rhum Nature Reserve, Inverness-shire.

This island Reserve (26,400 acres), established following purchase by the Conservancy in 1957, is of outstanding importance because of the wide opportunities it offers for research in climatology, geology, botany and zoology, particularly relating to the rehabilitation of the land with its flora and fauna.

The vegetation of the island has special interests with regard to the plants associated with the distinctive ultra basic rocks for which Rhum is famous. A good deal of botanical exploration has been carried out on the island and accounts of species and their distribution have been published, notably by J. W. Heslop Harrison (1939, 1941, and 1951) and by Clarke (1956). Permission is required to visit parts of Rhum beyond the Loch Scresort area.

Caerlaverock Nature Reserve, Dumfriesshire.

The Caerlaverock Reserve, of 6226 acres, was established by an Agreement in 1957 for the purpose of conserving a good sample of the great Solway Merse with its characteristic salt-marsh vegetation, and to give much-needed protection to the wildfowl frequenting the area. Very useful ecological studies relating to the reclamation of land along the Solway can be carried out readily within the Reserve. An invaluable paper on the plant ecology of the Merse (including some reference to its fauna) was presented by Morss (1927).

During 1958 four areas were declared Nature Reserves; two, Loch Druidibeg and Rannoch Moor being established by purchase, one, Tynron Juniper Wood by lease, and the fourth, Clairinsh, by Nature Reserve Agreement.

Loch Druidibeg Nature Reserve, South Uist, Inverness-shire.

This Reserve comprises 2,577 acres in the northern part of South Uist, and is of high ornithological importance, especially as the chief breeding place of the grey lag goose in Britain, but its vegetation is also of considerable interest, notably that of its ungrazed islets which await thorough ecological investigation.

Rannoch Moor Nature Reserve, Perthshire.

This portion, 3,485 acres, of the great moor of Rannoch, was acquired as a good sample of shallow high-altitude blanket bog, complementary to the bog land already conserved at the Silverflowe Reserve, referred to above. *Scheucheria palustris*, often in close association with *Carex limosa*, is well represented within the area.

Tynron Juniper Wood Nature Reserve, Dumfriesshire.

Here, within an area of 12 acres, is the best example of juniper woodland surviving in the South of Scotland. The bushes are tall, up to 10 ft. or more, and form a compact wood now protected by a fence, on a fairly steep slope above the west side of the road between Penpont and Kirkland.

Clairinsh Nature Reserve, Stirlingshire.

This small island (15 acres) in Loch Lomond, was declared a Nature Reserve because of its remarkably unspoilt and regenerating oakwood with a rich ground flora. Very few naturally-

developing and undisturbed oakwoods now survive in Scotland and this Reserve is unique of its kind.

Management Plans have been prepared or are in course of preparation for all the Nature Conservancy's Reserves and steady progress is being made towards the establishment of several new Reserves*.

SITES OF SPECIAL SCIENTIFIC INTEREST.

Over 200 Sites of this category in Scotland have already been notified to owners and to Local Planning Authorities in accordance with Section 23 of the National Parks and Access to the Countryside Act, 1949. Many of these Sites have been scheduled mainly or partly because of the occurrence within them of interesting plant communities or rare species likely to be endangered by possible changes in land use.

CONCLUSION.

A good deal has been accomplished, principally during the past ten years, in the task of organising along scientific lines the conservation of our native Scottish flora. The work for this cause must develop and continue through further research and education. The aims of conservation are both educational and economic. The educational aspects involve preservation of interesting samples of natural vegetation without affecting adversely the essential needs of agriculture, forestry and other interests. In biological training there are obviously no substitutes for observations and experiments in the field. Schools and Universities generally have come to appreciate more and more the value of field work in their curricula for the natural sciences and the recent establishment of National Nature Reserves has considerably encouraged and facilitated organised ecological investigations. The ever increasing numbers of amateur naturalists, too, must be considered and supported in their field studies which have added so much to our scientific knowledge of the wild countryside, and brought delight and solace to many otherwise heavily engaged with indoor activities.

*The Sands of Forvie Nature Reserve (1,774 acres) in Aberdeenshire was established by a Nature Reserve Agreement on 22nd January, 1959, bringing the number of National Nature Reserves in Scotland up to 20 with a total area of 100,401 acres.

The economic aspects of conservation are, of course, often interlinked with the educational aspects in so far as applied science is ever dependent on fundamental investigations and the pursuit of knowledge for its own sake. But the economic side of conservation is probably most evident when we have to consider problems of erosion and flooding, the management of natural woodlands and pastures, the control of pests, and all the safeguards which must be taken so as not to upset to our detriment the "balance of nature".

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JOHN WALKER, D.D., F.R.S.E., 1731-1803.

A NOTABLE SCOTTISH NATURALIST.

By GEORGE TAYLOR

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"In the posthumous works of Dr. Walker, the celebrated professor of natural history in the University of Edinburgh, many important observations are communicated, illustrative of Scottish (*sic*) plants. In the *Essays on Natural History*, Edin. 1808, some of the rarer species found in Icolumbkil, Jura, the Basse, and Collington are enumerated, together with minute descriptions of several kinds of willows.

"It is impossible to mention the name of Dr. Walker without bewailing the loss which botanical fame has sustained. It is well known that he had explored the vegetable productions of Scotland, not merely with an industrious, but with a philosophical eye, and that he was more acquainted with the extent of our Flora than any dead or living botanist. But he neglected during his lifetime to publish his numerous observations . . . Many of his manuscripts are in a finished state, and ought to be given to the public. His herbarium, instead of being scattered about among different collectors, and parcels of his rarest specimens sold along with their herbaria, should be deposited in the museum of the college . . . Such, indeed, is the respect which we entertain (and it is not cherished inconsiderately) for the memory of this great but neglected naturalist, that we are persuaded, that had he, in his vigorous days, published a *Flora Scotica*, it would have placed its author among the first botanists of the eighteenth century."

These laudatory remarks appeared in the *New Edinburgh Review* of October, 1821, in an anonymous and highly critical article on W. J. Hooker's *Flora Scotica*. In 1859, in the first chapter of his *Lithology of Edinburgh*, the Rev. John Fleming revealed his authorship of this review and, in a further eulogy of Professor Walker's contributions to natural history he reprints the above statement and expresses "a deep-felt conviction that

but they will come safe to Hand. In the mean Time, it would give me real Pleasure if you would write me with the same Freedom I have ventured to do to you in the Course of Post, & send me a List of the British plants you still want in your Collection You may direct to y^r Rev. Dr Walker at Moffat, Scotland.

Imagine the Limits between the native and naturalised plants are not yet well determin'd. I design'd to have sent you a List of some that are recorded by Ray and Hudson, that I suspected greatly are not indigenous, but this I must defer to another Letter, & should be glad of your Opinion concerning them. Have you ever met with the *Elymus arvensis* Lin. The Specimen presented for it, in Budden's hort. succ. is not the Plant, but a maritime variety of the *Festuca repens* Linn. And I did not see it in any of the Collections of English Plants.

I can supply you with Specimens also of the *Thalictrum alpinum*. *Oryas octopetala*. *Cucubalus acaulis*. *Saxifraga oppositifolia*, *stellaris aizoides*, *Lycopodium* & some other rare alpine plants.

I found lately a new Genus of the Musci, a very extraordinary Plant nowhere recorded, of which I hope to send you some account in my next.

I am in the mean Time with great Truth & Esteem

Dear Sir

Your most obedient
and most humble Serv^t

Moffat 30 Oct^r 1766.

John Walker

justice has not been rendered to his memory".† Fleming's assessment of Hooker's work is only cogent to the present paper in so far as he deplores Hooker's neglect to consult Walker's published records of Scottish plants. Fleming's strictures are probably deserved.* The omission by Hooker of any reference to Walker's treatment of *Salix*, with descriptions of several new species, is particularly surprising. From my own scrutiny of Hooker's *Flora Scotica* I have extracted 23 records attributed to Walker but these may well have been communicated by Robert Maughan, a keen Edinburgh amateur botanist of the day who, according to a footnote of Hooker's (Part I, p. 270) had access to Walker's herbarium after his death. But Hooker was not alone in overlooking Walker's work—such disregard and lack of appreciation prevailed among his scientific contemporaries and successors in the land of his birth and in the city where he taught, and have largely persisted to the present time.

Many examples of what seems wilful neglect may be cited but I shall only mention one or two. Walker was a correspondent of Richard Pulteney** but, apparently, was not deemed worthy of mention in the chapter concerning Scotland in his *Sketches of the Progress of Botany in England* (1790) though there is some excuse, as Walker's main works were only published posthumously. There is less justification for the scant notice given by J. E. Smith to Walker's botanical contributions. When Smith went to Edinburgh in 1781 to study medicine,

†In his *History of British Animals* (1828) 550, Fleming described the genus *Valkeria* remarking that it was "dedicated to the late Dr. John Walker, Professor of Natural History in the University of Edinburgh, a laborious and an accomplished naturalist".

*Another severely disparaging and anonymous review of Hooker's work was printed in *The Edinburgh Philosophical Journal* (1822) 6, 145-156. At places it betrays a certain national intolerance that the book should have been done by "a native of England".

**In the Pulteney correspondence preserved in the Linnean Society there is a letter dated 29th October, 1765, from Sir William Watson to Pulteney in which it is stated that "Dr. Walker of Moffat is also come to London He has collected a vast number of plants several of which he says are nondescript, and many thought not to be produced in Great Britain. He stays only a few weeks here a great part of which will be spent in the British Museum among the dried plants I believe he intends to publish a *flora Scotica*".

Walker, who was Professor of Natural History, gave the young student every encouragement and allowed the Natural History Society, of which Smith was a founder member and president, the use of his museum, books and specimens. In a letter to his father (15th April, 1782) Smith characterises Walker as a "most amiable, worthy and ingenious man".

There can be little doubt that Smith, who was also entertained by Walker at his home in Moffat, was aware of the professor's botanical research and had opportunities to examine his herbarium. In a letter to T. J. Woodward dated 28th September, 1782, Smith mentions that "Dr. Walker has found a number of plants in Scotland which are not in Lightfoot: among them are *Rubus arcticus*, *Lysimachia thyrsiflora*, and the indubitable *Elymus arenarius*, which I have seen and examined." Smith, like Walker, had a special interest in the genus *Salix*, and his first partial revision of the British species was published in *Trans. Linn. Soc.* (1802), 6, 110, in order that the genus "should assume as regular a form as possible in the *Flora Britannica*".

At that time Walker's *Essays* containing his observations on *Salix*, though probably written between 1764 and 1774, were still in manuscript and were not published until 1808. Smith, while he had seen at least some of Walker's herbarium and had three specimens of willow in his own collection from Walker's garden at Moffat, may have been unaware of their common interest in the genus. This would certainly excuse the omission of any reference to Walker in the *Flora Britannica* (1804) but Smith practically ignored his work in the later treatments when he knew of Walker's studies in *Salix*. In his lengthy monograph in Rees's *Cyclopaedia* (1819) only two of Walker's species were cited. In his *English Flora*, 4 (1828) he presented a very full treatment of the genus and recognised 63 species. Walker's *Essays on Natural History* is among the books listed as used by Smith yet it is only mentioned once in the text. More surprisingly, only two of Walker's species are mentioned (one, *S. vaciniifolia*, without attributions to the original author) and a single record, *S. andersoniana*. In Sowerby's *English Botany*, in which the texts were written by Smith, the same neglect is evident, yet Smith (*Engl. Fl.*, 4, 165) complained of Hooker's perfunctoriness in the treatment of *Salix* in his *Flora Scotica*. "I should have hoped", he says, "that my excellent friend Dr. Hooker would

have given Mr. Crowe and myself credit for some accuracy of observation, and not have set almost all our labours at nought, without some practical knowledge, at least, of his own."

A noteworthy Scottish naturalist and the only one, so far as I have been able to trace, who attempted to account for Walker's willow species and records within the limited area in which he was interested, was Dr. George Johnston. He was a competent and scholarly botanist who was clearly conversant with Walker's work, and, like Walker, he made significant contributions to zoology as well as to botany.* In his earlier publication, *A Flora of Berwick-upon-Tweed*, Johnston includes only *Salix argentea* of Walker's, but he accounts for three species of marine algae which Walker had described.† In his incomplete *The Botany of the Eastern Borders* (1853) Johnston quotes frequently from Walker's *Essays* particularly in his discussions on trees and acknowledges Walker (*Fl. Berwick-on-Tweed*, 322) "as the best of all authorities on a question of this kind". Apart from *S. argentea*, Johnston in his later work mentions three of Walker's *Salix* species, referring them to synonymy.

Another Scot, J. C. Loudon, in his discursive introduction to *Salix* (in *Arboretum et Fruticetum Britannicum* (1838, 3, 1453 *et seq.*) refers to Walker's account but, apart from the two species enumerated by Smith, does not mention his described species. Elsewhere Loudon has lengthy references and quotations from Walker's *Essays*, especially in the second chapter of Volume I, which deals with the history of trees in the British Isles. Altogether the index credits Walker with forty citations throughout the four volumes of text.

Later botanists who worked on the genus *Salix* as represented in Europe have all either merely copied the meagre earlier references to Walker's species or ignored his work entirely. The British botanists, F. Buchanan W. White and E. F. Linton, who

* Johnston (*History of the British Zoophytes*, 1828, p. 252) remarks that Walker's *Essays on Natural History* "is an interesting volume which I have had occasion to regret was not more noticed in our Fauna and Flora".

† This is the more remarkable since Greville (*Algae Britannicae*, 1830) though referring in his introduction to Walker's classification, omits any mention of his described species. It may also be observed that no record of Walker's is given in Greville's *Flora Edinensis* (1824).

published accounts of the British willows, made no attempt to elucidate Walker's species. His synonymic citations and references, for example to Buddle's Herbarium in the British Museum, in some cases provide useful clues.

Walker's herbarium has not been traced since it was removed by his trustees from the University after his death, and in the absence of specimens it will be difficult to interpret Walker's willows. They are, however, very fully described and sometimes localized, and an attempt should be made to relate them to the taxa now recognised. This, of course, should also be done with the other species which Walker described.

Walker's paper on willows is entitled *Salicetum: the Botanical History and Cultivation of Willows*, and is included in his *Essays on Natural History and Rural Economy* published posthumously in 1808, though some title pages are dated 1812. This work and his *Economical History of the Hebrides and Highlands of Scotland*, together with the unpublished material preserved in the library of Edinburgh University, contain a wealth of botanical information of interest to British botanists. Besides descriptions of new species there are many early records and some effort should now be made to account for these.

It is true that Dr. Symers Macvicar (in *Ann. Scot. Nat. Hist.*, 1895, 257) expressed the view that Walker "has not, I think, received the attention his botanical discoveries deserve" and (in *Trans. Bot. Soc. Edinb.*, 1901, 22, 30) that he "has not received sufficient recognition. An account of his contributions to the natural history of Scotland would be interesting and instructive". Yet no thorough endeavour has been made by British botanists to study Walker's published work and to evaluate the records in his voluminous manuscripts. One would not have expected Walker's records to have escaped the notice of Trail and Druce who both prepared considerable historical surveys of Scottish botany and were both zealously interested in Scottish records. It is also surprising that Bayley Balfour, who was deeply concerned in tracing and preserving records and manuscripts relating to Scottish botany, failed to gain an appreciation of Walker's botanical studies and of his contribution to the knowledge of the Scottish flora. Balfour edited the *History of the Royal Botanic Garden, Edinburgh*, in which Walker is mentioned twice in letters with, in addition, a footnote reference by the editor (*Notes R.B.G.*



The Rev. John Walker, D.D. (about 1731-1804).

From an engraving in *The Naturalists' Library*,
Volume XII, 1842.

Edinb., 1904, 3, 24, 32). This volume also contains correspondence of John Mackay, Superintendent of the Royal Botanic Garden from 1800 till 1802, who travelled widely in Scotland in pursuit of his botanical studies at the time when Walker in Edinburgh was accumulating material for a flora of Scotland.* Mackay's letters contain some of the earliest records of Scottish plants which, like Walker's have not been fully recognised by later students. Balfour's further interest in early Scottish records is manifest in his publication (in *Ann. Scot. Nat. Hist.*, 1900, 169-174; 237-243; 1901, 37-48) of *Eighteenth Century Records of Scottish Plants* from the manuscript notebooks of John Hope, Regius Keeper of the Royal Botanic Garden, 1761-1786. This was reprinted in *Notes R.B.G. Edinb.*, 1907, 4, 123-192, with the addition of a list of plants collected in the neighbourhood of Edinburgh in 1765. Two of Walker's records appear in these lists.

Although Walker's botanical observations were practically ignored, he was regarded as an authority on agricultural and arboricultural matters and on these subjects was extensively quoted by contemporary and later writers. Such references have in many cases been found quite fortuitously and often in the most unexpected places. Additionally, search for Walker references has revealed a number of apparently authentic and interesting early records of Scottish plants. For example, in the so-called "Scenery" edition of Allan Ramsay's *Gentle Shepherd*, published in two volumes in 1808, there is incidental mention of Walker's part-authorship of the *Statistical Account of the Parish of Glencross* (Glencorse) and his works are also quoted in the volumes. Those interested in early records of Peeblesshire and Midlothian plants will find lists of species from eight localities in which scenes of *The Gentle Shepherd* are set, and a good map of the district

*Though Walker's field efforts had probably ceased towards the end of the 18th century, it was a period of great exertion in the botanical exploration of Scotland. Mackay, George Don and Robert Brown, among others, were very active. Brown enjoyed Walker's friendship and encouragement as a young student at Edinburgh and it was probably under Walker's influence that, at the age of 18, he presented his first paper on *The Botanical History of Angus* (later published in *J. Bot.*, 1871, 9, 321) to the Edinburgh Natural History Society in January 1792. Mackay, in one of his letters to Brown, refers to Walker as "our worthy friend", but Don, who only settled in Edinburgh in 1802 on his appointment as Principal Gardener of the Royal Botanic Garden, does not seem to have been associated with Walker.

is provided embracing part of the upper source of the North Esk which here is the boundary between the two counties. There is no disclosed authorship to this edition but help in the preparation of the botanical lists by Mr. P. Neill, one of the original members of this Society, is acknowledged. One of the lists, however, is attributed to Dr. Pennecuik whose *Geographical and historical description of the Shire of Tweeddale*, with his poetical works, was published in 1715. This early work of Pennecuik contains a number of Peeblesshire records and an alphabetical list of unlocalised rare plants of which only a few are included in F. R. S. Balfour's chapter on Botany in his *History of Peebles* (1925). Pennecuik's works were reprinted by A. Allardice exactly 100 years after their original publication. In this reprint there are copious anonymous notes with frequent quotations from Walker and lengthy botanical references. Indeed, some of these citations and remarks are identical with those already noticed in the 1808 edition of *The Gentle Shepherd*. Furthermore, seven of the eight plant lists are also reprinted from that work with minor differences as, for example, the insertion of the date "in 1814" at the head of the Habbies How list. It seems fairly certain that the annotations on these works were closely concerted and may well have been written by the same person.

Walker's manuscripts preserved in the library of Edinburgh University cover a wide range of his interests and activities. Of particular importance to botanists are the volumes in which Walker, year by year, has noted interesting records, a good many from Edinburgh and neighbourhood supplied by Mr. Yalden, who also provided lists to Lightfoot which were used in his *Flora Scotica*. The record of *Lysimachia thyrsoiflora* which was mentioned by Smith and referred to above appears in the volume of Walker's MS. dated 1768. There (on p. 114) he states, "This plant I found in the Canon Mill Bog at Edinburgh in Summer 1750, and I have a specimen of it prepared since that year but without the flower". He also records *Utricularia vulgaris* in 1750 from the same locality. These are two of many examples of the early records to be found in the manuscript—and all should eventually be published as they would certainly form a valuable chronicle. The records of species in his printed works should also be extracted and published. As a guide to these records of indigenous plants, where these are less vaguely localized, the following citations may be helpful.

Essays on Natural History and Rural Economy.

History of the Island of Icolumbkil (Iona) pp. 180, 182, 184, 186, 188, 190, 197, 198.

History of the Island of Jura pp. 242, 245, 246, 247, 248, 251, 254, 255, 257, 263, 265, 267, 272, 274, 275, 277, 280.

A description of the Basse and its productions pp. 289-300.

The Natural History of Loch Leven p. 380.

Salicetum. The botanical history and cultivation of Willows pp. 424-469.

Statistical Account of the Parish of Collington pp. 564, 595-596.

Economical History of the Hebrides and Highlands of Scotland.
Vol. 1, pp. 132, 343, 375, 380; vol. 2, pp. 33, 135, 261, 263, 278, 279.

In this paper it seems advisable to reprint the descriptions and, where indicated, the provenance of Walker's validly published species and varieties, as his works are not easily available and the information should be useful to botanists. The names of the *Salix* species will be included in the forthcoming supplement of the *Index Kewensis* and the other new species will appear in the following supplement.

ESSAYS ON NATURAL HISTORY AND RURAL ECONOMY.

p. 242. *Scirpus tetragonus*, culmo tereti levi vaginato, sub vagina tetragono striato, spica ovata sexflora.

Scirpus equiseti capitulo majori alter. Scheuchz. gram., p. 361, tab. 7, f. 17?

p. 244. 1. This plant was found in a boggy soil near the sea shore in Jura, and is not mentioned either in Ray's Synopsis or Linnaeus's system. The description given by Scheuchzer does exactly answer the plant, but his figure exhibits more flowers than are to be met with in its spike, which are pretty constantly only six in number. Though a separate species, a nicer attention is required to distinguish it from other plants of the genus, than what has been usually paid by botanists to the gramineous tribe.

2. It partakes of the habit and characters of the *Scirpus palustris*, *cespitosus*, and *acicularis* of Linnaeus, but of these, it approaches nearest to the *palustris* from which, likewise, it is essentially different. The *palustris* is more than double its size; and the spike larger, with a much greater and indefinite number of flowers, while those of the *tetragonus* are determined to six in number. The stalk of the *palustris* is declined, of a compressed

shape, but round, so far as the sheath extends. Whereas the stalk of the *tetragonous* is erect, perfectly round, and so far as the sheath extends, distinctly quadrangular.

- p. 245. II. *Juncus sylvaticus*, foliis planis pilosis, umbella supra decomposita floribus subsessilibus. Huds. angl., p. 132, n. 11.

Juncus foliis planis pilosis, corymbo decomposito floribus aggregatis sessilibus. Lyons Fascic., p. 31.

Gramen nemorosum hirsutum latifolium maximum. Raj. syn., p. 416, n. 4. Raj. hist., 1292. Buddl. hort. sicc., vol. 12, fol. 23.

Broad leaved hairy Wood Grass.

- III. β *Juncus montanus* panicula fastigiata subtrifida decomposita sparsa erecta.

Gramen hirsutum latifolium minus. Bauh. pin., p. 7, n. 2. Theat., p. 102, fig. 2. Moris. hist., 3, sect. 8, tab. 9.

Hoary Mountain Rush.

- p. 246. 1. The *Juncus sylvaticus* is common in all the woody parts of the Hebrides, and is indeed the most frequent plant in all the woods of Scotland. It is improperly considered by Linnaeus as a variety of his *Juncus pilosus*, and is very well distinguished by Mess. Hudson and Lyons, as a distinct species from that plant.

- p. 246. 2. The *Juncus montanus* is a variety, not of the *pilosus*, as Linnaeus has it, but of the *sylvaticus*. It was first considered as such by Caspar Bauhinus, and the figures given of it by him and Morison, are both characteristic enough of the plant. It varies remarkably from the *sylvaticus* in the place of its growth, which is no doubt the cause of any other differences to be observed between them. The *sylvaticus* grows always under the shade of rocks or trees, but the *montanus* was found on the very summit of the most westerly mountain in the island of Jura, at the height of two thousand three hundred and forty feet above the level of the sea, on the 27th of June, on which day it had unfolded its first flowers. It was since found on the top of a mountain, of about the same height, on the 17th of July, when its flowers had begun to decay.

- p. 255. *Pteris britannica* frondibus subbipinnatis; foliolis suboppositis lanceolatis pinnatifidis; lobis oppositis ovatis obtusis integerrimis.

Filix mas vulgari aliquatenus accedens pinnulis rigidioribus et acutioribus quarum margines lineis seminalibus ex tuberculis pulverulentis compositis observantur. Buddl. hort. sic., vol. 3.

Filix non ramosa nostras, pinnulis brevibus acutioribus integris, nonnihil falcatis, punctis ferrugineis ad oras pulverulentis. Pluk. amalth., p. 91.

Filix fontis admirabilis ad marem vulgarem non ramosum accedens non dentata. Bauh. hist., vol. iii, p. 731. Raj. hist., p. 145.

p. 257. 1. Of the numerous genus of *Pteris*, this plant makes only the third species hitherto discovered in Europe. It was found in the hollow sheltered parts of Jura, intermixed with the common fern, and has since been discovered near Oxford by my friend, the Reverend Mr. Sheffield, Fellow of Worcester College.

2. It is a plant which has very much escaped the notice of botanists, by its near resemblance to the *Polypodium filix mas*, Linn. or common male fern, and it was by accident I happened to distinguish them. By laying hold of a bunch of fern, in clambering up a precipice, the marginal fructification of this plant caught my eye, which showed it to be very different from the common fern. But when this is once known, the two plants are easily distinguished by their external habit; the *Pteris* being of a less size, with a more narrow and less divided leaf, and of a brighter green colour.

p. 263. X. *Bryum britannicum*, antheris erectis pyriformibus, collo contracto, ore ciliato, surculis simplicibus, foliis lanceolatis.

Bryum ampullaceum, foliis serpylli pellucidis, collo crassiore. Dill musc., p. 344, T. 44, f. 4.

Bryum erectis gigartinis capitulis, foliis serpylli pellucidis obtusis. Raj. syn., p. 93, n. 5, Tab. f. 2.

Bryum trichoides palustris aestivus, capitulis nigris erectis, collo luteo fimbriato. Richards, Raj. syn., *ibid*.

1. It was found in boggy ground, among tall heather, upon one of the hills, in ascending to the paps of Jura, at about one thousand two hundred feet of perpendicular height above the sea.

p. 264. 2. It is a plant of which we find no notice taken by any botanical writer except Ray and Dillenius. It seems to have been hitherto discovered only in Britain, and is one of the rarest plants of the genus, that has yet occurred to the British botanists.

3. It is sufficiently distinguished by Dillenius's description; and his figure is much better than that in Ray's Synopsis, which represents the leaves too oval, and the ciliae or hairs at the orifice of the anthera of too large a size, and too few in number.

4. It appears to be a plant of an alpine nature, and differs from most of the other species of *Bryum* in the lateness of its growth. It vegetates vigorously, and produces its flowers in summer, when most of the other *Bryums* are decayed. On the 27th of June, only a few of its antherae were blown, the greater part being very young, with their calyptrae or caps still remaining upon them.

5. It approaches in its habit and characters both to the *Splachnum ampullaceum* and the *Bryum pyriforme* of Linnaeus. Having no umbraculum, however, or umbrella, it cannot be referred to the *Splachnum*; and from the *Bryum pyriforme* it is distinguished, both by the shape of its anthera, and by its orifice being ciliated, which in the *pyriforme* is plain.

- p. 265. XI. *Bryum laterale*, Surculis scopariis, foliis setaceis secundis, pedunculis lateralibus surculo brevioribus, antheris sphaericis.
- p. 266. It was found upon a moist shady rock, in a deep gully, upon one of the hills of Jura, and must undoubtedly be a very rare plant; having escaped the researches both of Dillenius and Linnaeus. The turf it forms resembles that of several other kinds of *Bryum*; but its antherae, though very peculiar, are not to be seen, because of their lateral position, till it is pulled up, and the stems are separated from each other, which may be the reason why it has so much eluded the eyes of botanists. It approaches nearest to the *Bryum pomiforme* Linn. but it is a quite different species.
- p. 267. XII. *Lichen quartzosus*, leprosus niger ramosus radiatus, ramis setaceis tenuissimis, tuberculis atris hemisphaericis.
- p. 268. 1. This minute plant has been observed upon the tops of several of our highest montains in Scotland, but always upon stones of quartz: and the *Basanites jurae*, a stone of the quartz kind, of which the paps of Jura are composed, was found entirely covered with it in many places, especially on the very summits of the mountains.
2. It is a distinct species of Lichen, which we find not observed by any writer. Its younger spots, when the ramifications are distinct, have a very elegant appearance, when spread upon pure white quartz, and exactly resemble the arborescent appearances so much admired in the stones of Mocho. They are so fine as scarce to appear raised above the surface: they are not to be separated from it; and seem more like stains natural to the stone, than plants. The minuteness and delicacy of the plant seem to require a very smooth and hard surface for the place of its growth, which is perhaps the reason why it is so generally attached to quartz.
3. Of all plants hitherto discovered, it is one of the most minute, being scarcely discernible from the substance of the stone upon which it grows; and may be considered as one of the links, that connect the vegetable world with inorganized matter. The little *Bryum truncatulum* of Linnaeus, the Hyssop of Solomon, according to Hasselquist, is a cedar compared to this plant.
- p. 272. XV. *Chara scotica*, inermis caulibus dichotomis glabris, ramulis verticillatis simplicibus scabris scruposis: terminalibus scopariis.
- p. 273. A few plants of it were found growing among the rushes, in one of the bogs of Jura. The place, though moist, was not watery, and the plant was growing erect in the air, and not under water like the other sorts of *Chara*. No fructification appeared upon it, yet its habit shows it unquestionably to be a *Chara*, of which we have hitherto found no vestige in any botanical writer.

- p. 274. XVI. *Ulva fastigiata*, tubulosa fusca lubrica ramosa, ramis fastigiatis simplicibus teretibus inarticulatis.
Bundled Laver.
- p. 275. There does not appear to be either description or figure of this plant in any botanical writer. It is very common upon the shores of Jura, and most of the other western islands, and grows in the basins of sea water left among the rocks upon the recess of the tide.
- p. 275. XVII. *Bombycina jurensis*, caule continuato, ramis teretibus subpennatis; tuberculis lateralibus spongiosis, apicibus subsimplicibus denticulatis.
Fucus marinus purpurascens parvus, caule et ramulis seu foliolis teretibus. Raj. syn., p. 50, n. 50. Buddl. hort. sicc., vol. 1, fol. 16, fig. 3.
Jura Silk Weed.
- p. 276. It is a very rare plant upon the shores of Scotland, and one specimen of it thrown up by the sea in Jura was the only one found in all the western islands.
- p. 277. XVIII. *Bombycina deuceledonica*, ramis binatis secundis, tuberculis sessilibus axillaribus.
Deuceledonian Silk Weed.
- p. 279. No figure or description of this plant can be observed in any of the botanical writers. It was found at sea, off the island of Jura, and taken up in the same manner, in sailing between the Lewes and the mainland of Scotland. In both places it was found in a mass, so twisted and interwoven, as not to be easily unravelled, and very much resembles the black fibrous roots of trees. In this resemblance, it exactly agrees with the Fucus radicibus arborum fibrosis similis. Ray. syn., p. 49, n. 45, but is a very different species from that plant.
- p. 426. II. *Salix malifolia*.
S. foliis ovatis, acuminatis, subtus tomentosis, margine undulato subintegro.
Salix (Caprea) foliis ovatis rugosis: subtus tomentosis, undatis, superne denticulatis. Linn. Sp., p. 1448, n. 28. Var. a. Flo. Lapp., n. 365. Tab. 8, fig. 8.
- p. 427. Salix Caprea, Hoffman. Hist., p. 25, tab. 3, fig. 1, 2; tab. 5, fig. 4.
Salix latifolia inferne hirsuta. Bauh. Hist., I, p. 215 fig.
Salix Caprea latifolia. Ger. em., p. 1390, fig. 4.
Salix Caprea rotundifolia. Tradescant. mus., p. 164.
Scot. Apple-leaved Willow.
Angl. Goat broad-leaved Sallow. Ger. round-leaved Sallow.
Chestnut-leaved Willow.
Great Goats Willow, Tradescant.

Descriptio

Arbor 30 pedum.—Rami annui et annotini virides glabri.—Folia novella utrinque villosa, versus basin ferruginea, marginibus revolutis.—Folia matura magna ovata acuminata, supra glabra, subtus albo-tomentosa, ad petiolum inaequalia, margine subintegro undulato.—Stipulae auriculatae acutae integrae.

Mas.—Amenta terminalia ovata, dum fumant ferè globosa.

Involucrum foliolis 5 lanceolatis integris villosis.

Squamae nigrae albo-villosae.—Stamina duo.—Antherae luteae.

Nectarium, Glandula cylindrica truncata, guttulam limpidam separans.

Foemina.—Germen pedicellatum villosum.—Stigmata duo bifida lutea.

Nectarium ut in mare.

Place.—It is frequent in our natural woods, and is often p. 428 introduced into plantations. In the mountain gullies of Annandale and Nithsdale, it is to be seen growing at a height from one thousand two hundred to one thousand five hundred feet above the level of the sea.

p. 431. III. *Salix amnicola*. *Helix* Linn.

Salix Helix et *amnicola* characteribus sequentibus discrepant.

Helix, N. *purpurea* Linn.

amnicola N.

- | | |
|--|--|
| 1. Arbor 20 pedalis, caudice ramisque erectis. | 1. Frutex humilis, caulibus ramisque obliquis decumbentibus. |
| 2. Rami annui praelongi amaene lutescentes. | 2. Rami annui breviores purpurei. |
| 3. Folia novella opposita. | 3. Folia novella alterna. |
| 4. Folia matura leviter serrata. | 4. Fol. mat. insigniter serrata. |
| 5. ——— supra dilute viridia, subtus pallidiora. | 5. ——— supra saturate viridia, subtus glauco-coerulea. |
| 6. Folia omnia saepe opposita, inferiora raro alterna. | 6. Folia omnia saepe alterna inferiora interdum opposita. |

Salix Helix et *amnicola* characteres sequentes habent communes.

Rami annui tenues glaberrimi tenacissimi.—Vernatio equitans.—Stipulae nullae—Folia novella glabra viridia, versus basin ferruginea.—Puncta duo infra basin petioli primum albida, postea ferruginea.—Folia matura oblongo-lanceolata, acuminata, glaberrima, serrata, serraturis glandulosis, versus basin et in ipso acumine intergra. Flos monandrus.

p. 435. V. *Salix argentea*.

S. foliis integerrimis sessilibus obovatis eglandulis utrinque tomentosis, apicibus oblique reflexis, stipulis pedicellatis.

Salix pumila foliis utrinque candicantibus et lanuginosis. Raj. syn., p. 447, n. 3, tab. 19, fig. 3.

Descriptio.

Frutex bipedalis quatuor pedalis procumbens. Rami annui et annotini teretes tomentosi albid. Folia sessilia integerrima obovata acuta crassa, sursum secunda, eglandula utrinque tomentosa, argentea, sciz. albo cum splendore praedita. Apices foliorum ita oblique reflexi sunt, ut emarginati appareant. Stipulae pedicellatae ovatae acutae integrae.

p. 436. Mas.—Amenta alterna, interdum ramulis supremis opposita. Squamae lutescentes.—Antherae luteae.

Place.—It grows on the sandy shores of the Rins of Gallo-way, and of West Ross; also in the plantations on the sandy shore at Tynningham in East Lothian; and there, as in other places, appears altogether as a maritime plant.

1. This is the Willow that grows near Sandwich in Kent. It is probably meant by several writers; yet the above name of Ray is the only one that with Certainty can be applied to it, though the figure in the Synopsis is far from being satisfactory.

p. 437. VI. *Salix amerina*.

BRIT. Amerine Willow. Poplar Willow. Cane Willow.

Descriptio.

Arbor triginta pedum—Truncus et brachia cinereo-alba glabra nitida—Rami annui rubro-virides; annotini albid. glabri nitidi. Folia novella glaberrima bicoloria, sciz. viridia, versus basin ferruginea. Folia matura lanceolata glaberrima, amoene viridia, subtus pallidiora, serrata; serraturis glandulosis. Ad ipsum apicem et basin serrata. Stipulae uniauritae ovatae acutae persistentes, serraturis glandulosis, caducae. Hybernaculum gemmae foliosae, e squamis tribus constat: una interiore; duabus exterioribus inaequalibus.

p. 438

Mas.—Amenta tenuia lutescentia, medio rami annotini posita. Squamae lutescentes albo-ciliatae. Stamina duo. Antherae luteae. E surculo, amenta producit anno quarto.

Place.—Brought originally from England or from abroad, but long cultivated in Scotland as a basket Willow. It is probably a native of the east, and perhaps of the southern parts of Europe.

1. It is distinguishable from all the Willows by its white smooth burnished bark, which is exactly like that of the black poplar, and from which it has generally obtained the name of the poplar Willow. For the same reason it is called the cane Willow by others.

2. It may be the *Salix candida* of Theophrastus, but with greater probability it may be presumed to be the *Salix amerina* of Pliny, who applies to it the name of Candidior, evidently

p. 439 from the whiteness of its bark. It seems also to be the *Salix amerina* of Dalechampius, well known in the vineyards in the eastern parts of Europe, and also in France, where it is introduced for supporting the vines.

3. It grows in great abundance, and with great appearance of being a native, upon the river of Eden at Mellerstain in the Merse; but has undoubtedly been introduced, along with many other exotic trees, in the plantations about that fine place. One tree of this sort, upon the river below the house, was measured in September 1795, and found to be four feet ten inches in circumference, four feet above the ground, and thirty feet high.

4. Like the other Willows of a southern climate, its growth is continued late in autumn, till it is interrupted by the frost.

p. 440. VII. *Salix phloragna*.

S. foliis glaberrimis lanceolatis, serraturis glandulosis, stipulis uni-auritis ovatis, floribus triandris.

Salix folio amygdalino utrinque aurito, corticem abjiciens. Raj. syn., 2, p. 292, n. 6—Ed. 3, p. 448, n. 10.

Salix foliis eliptico-lanceolatis, utrinque glabris serratis appendiculatis. Gmelin. Flor. Siber. tom., 1, p. 155, tab. 34, fig. 3.

Salix (auriculata) foliis serratis glabris lanceolatis omnibus alternis. Miller Dict., n. 9.

Salix foliis glabris, eliptico-lanceolatis, serratis, stipulis dentatis, julis gracilibus, triandris. Haller Hist., n. 1637.

Brought to Scotland from different parts of England and Ireland by the names of the Goldstone Willow, Irish Willow, Brown Rod, and Spanish Willow.

Descriptio.

Arbor mediocris.—Rami annui angulati virides glaberrimi. Folia novella unicoloria viridia glaberrima. Folia matura lanceolata glaberrima serrulata, serraturis glandulosis, supra viridia, subtus pallidiora. Stipulae uni-auritae strictae latae ovatae acutae persistentes, margine glanduloso.

p. 441. *Mas*.—Amenta mascula pluria versus apicem ramulorum, post vernationem erumpentia. Gemmae foliiferae ad basin gemmarum amentiferarum erumpunt. Amentum sesquiunciale cylindricum album. Involucrum tetraphyllum, foliolis ovato-lanceolatis integris stipulaceis persistentibus, ad basin exterius villosis. Squamae ovatae obtusae concavae albae. Stamina tria. Antherae luteae.

Foemina.—Amenta foeminea post vernationem erumpunt. Amentum sesqui-unciale cylindricum tenue. Involucrum tetraphyllum, foliolis stipulaceis, persistentibus, foliis arboris prorsus similibus. Squamae ovatae obtusae rugosae albo-virides glabrae muticae. Stigmata duo bifida. Ad basin gemmae amentiferae, una v. altera gemma foliacea serotina erumpit.

p. 441. 1. Though this Willow has three stamina, it appears to be a different species from the *triandra* of Linnaeus. He quotes indeed the above name and figure of Gmelin, which evidently belong to this plant, but still there is reason to suppose that the *triandra* meant by Linnaeus is a different species, or, at least, that there is another triandrous Willow.

2. It has no appearance of being a mountain or Alpine Willow. It may grow in Siberia, but it grows also upon the Rhone. It looks like a native of the southern parts of Europe, and though probably not indigenous, has been long cultivated in England. Like the other southern Willows, its shoots continue growing till after the 15th September, and even till they are cut down by the frost. It is of a strong and vigorous growth, and rises up in a few years to be a tree twenty feet high. At Newhailes in Mid-Lothian it has been seen to throw up a shoot ten feet long in one season.

p. 443. VIII. *Salix rubra*.

S. Foliis ovatis acuminatis glabris glanduloso-crenatis, margine undulato, stipulis uni-auritis.

Scot. The Red Saugh.

Descriptio.

Arbor 40 pedum. Folia ovata, apice acutiusculo, sciz. acumine brevissimo, serrato-crenata, basi inaequalia, leviter tomentosa, margo foliorum undulatus, apex interdum obtusiusculus. Rami annui pubescentes subrubri; annotini lutescentes glabri. Folia novella basi ferruginea. Vernatio revoluta. stipulae uni-auritae ovatae acutae persistentes, margine glanduloso.

Mas.—Amentum ovatum ante explicationem rufum. Antherae ante fumationem rubrae, postae luteae. Fumat 1 Maji. Involucrum sex foliolis inaequalibus ciliatis. Squamae fusice villosae. Nectarium, glandula cylindrica minima truncata, guttulam limpidam separans. Antherae duae.

Foemina.—Amentum et nectarium ut in mare. Germen pedicellatum villosum. Stigmata due bifida.

p. 444. *Place*.—This Willow was first observed in the year 1758, at Woodhouselee, near Edinburgh. Plants of it are still to be seen in the remains of the natural woods in the parishes of Lasswade and Collington. It is frequent also in the woods of Annandale, Nithsdale, and many other places.

p. 446. IX. *Salix rubigo*.

S. foliis crenatis ovatis acutis exstipulaceis, utrinque villosis sericeis, crenis glandulosis.

Descriptio.

Caules bipedales quinquepedales virgati divergentes patuli graciles nudi. Rami annui tomentosi, annotini glabri. Folia sessilia ovata acuta, utrinque villosa sericea, leviter crenata,

sciz. crenis duabus tribusve, cum glandula villis immersa. Stipulae nullae.

Poeminea.—Amenta extremitatibus ramulorum, masculo absente, abortiva cadunt.

Argentea

- α Caules firmi crassi.
- β Rami annotini tomentosi.
- τ Folia obovata integerrima eglandula.
- δ Stipulae ovatae acutae integrae.

Rubigo

- α Divergentes patuli graciles.
- β ——— glabri.
- τ Ovata leviter crenata glandulosa.
- δ Exstipulata.

Place.—First found anno 1795, by Mr. Arthur Bruce in the head of Teviotdale, at a great height above the sea, in a bog upon the estate of Mr. Douglas of Cavers.

p. 449. XI. *Salix halleri*.

S. foliis integris eglandulis, ovatis acutis rugosis, supra glabris, subtus tomentosis.

Salix foliis integerrimis, ovatis lanceolatis, subtus sericeis, julis tomentosis. Haller. Hist., vol. ii, p. 307, n. 1642.

Descriptio.

Salix Lapponum et Halleri characteribus sequentibus discrepant.

Lapponum.

1. *Rami annui* tomentosi albi.
2. *Folia novella* utrinque tomentosa unicoloria alba.
3. *Stipulae* acutae.
4. *Folia matura* laevia supra albida, subtus alba, utrinque tomentosa.
5. *Folia*, tactu mollia.

Halleri.

1. Glabri virides.
2. Supra viridia glabra, subtus tomentosa albida, basi ferruginea.
3. Ovatae obtusae.
4. Rugosa, supra saturate viridia glabra, subtus viridi-albida tomentosa.
5. Scabra.

Place.—This Willow was sent about the year 1770 from Switzerland, along with other alpine plants, to the late Sir James Nasmyth. It has been kept, for many years, in the same garden with *lapponum*; but the different characters of the two plants, as marked here in their names and descriptions, continue always the same.

p. 451. XII. *Salix Americana*.

S. foliis serratis utrinque glabris lanceolatis: serraturis glandulosis, stipulis minimis ovatis acutis.

Descriptio.

Frutex humilior.—Rami annui glabri virides graciles lentissimi: annotini purpurei.—Vernatio equitans.—Folia novella unicoloria, sciz. albido-sericea.—Stipulae minimae ovatae acutae caducae.—Petioli elongati.—Folia matura exstipulacea lanceo-

lata elongata, utrinque glabra, supra dilutè viridia, subtus pallidiora, margine recta serrulato: serraturis glandulosus.—Folia ad apicem et ad basin serrulata sunt.

Place.—It was brought from America by Lord Loudon; but no name of any author has occurred, that with certainty can be applied to it.

p. 452. XIII. *Salix concolor*.

S. foliis undulatis glabris oblongis acuminatis crenatis: crenis glandulosus, paginis concoloribus.

Description.

Statura arborea.—Rami annui glabri rubro-virides: annotini fusco-purpurei.—Vernatio equitans.—Folia *novella* glabra unicoloria viridia.—Stipulae latae uniauritae acutae persistentes, serratae: serraturis glandulosus.—Petioli elongati rubro-virides.—Folia *matura* oblonga acuminata diaphana, utrinque glabra concoloria, margine undulato crenato, cum glandula in crena. Folia ipso acumine, et ad basin integra.

Place.—It was found in the collection of Willows at Loudon; but it did not appear with certainty, from what country it had been brought.

p. 454. XIV. *Salix aequivoca*.

S. foliis integris oblongis acutis, glandulis marginalibus, stipulis uniauritis ovatis acutis.

Description.

Statura arborea.—Rami annui rubricantes tomentosi: annotini purpureo-nigri.—Vernatio revoluta.—Folia *novella* albida leviter pilosa, basi ferruginea.—Stipulae parvae uniauritae ovatae acutae persistentes, margine glanduloso.—Folia *matura* hexapla integra oblonga acuta, margine glandulis adperso at vix serrato, supra glabra, subtus albido-tomentosa.—Ramuli aestivi foliis obovatis obtusiusculis.

Place.—It was found among the Willows at Loudon Castle; but it was not known from whence it had been brought; nor does it appear with certainty in any author.

p. 455. XV. *Salix ligustrifolia*.

S. foliis integris eglandulis linearibus acuminatis exstipulaceis.

Salix fissa, foliis integris, oblongo-lanceolatis, acuminatis glabris. Hoffmann. Hist., p. 61, Tab. 13 et 14.

Salix tristis, exstipulacea, foliis lineari-lanceolatis petiolatis rugosis subtus tomentosis. Hort. Kew., vol. iii., p. 393, n. 24? Lumnitzer. Flor. Poson., p. 443, n. 976.

Description.

Frutex debilis vix humani altitudinis.—Rami annui graciles filiformes virides glabri: annotini fusci.—Vernatio equitans.—

Folia *novella* unicoloria viridia glabriuscula.—Stipulae nullae.—Folia *matura* linearia acuminata, integra eglandula, supra saturate viridia glabra, subtus albida minutissimè pilosa.—Punctum rubrum unum alterumve, infra basin petioli.—Gemmae in exillis foliorum rubrae.

Place.—It seems to be a native of the midland and southern parts of Europe. Along with other live Willows, two plants of this species were sent me by Professor Thunberg, anno 1788, from the Upsal garden, but without any name, and both turned out to be females.

p. 460. XVIII. *Salix vacciniifolia*.

S. foliis serratis glabris, serraturis glandulosis, stipulis ovatis obtusis convexis integris.

Salix Alpina, alni rotundo folio, repens. Boccon. Mus., pars 2, tab. 1?

Descriptio.

Frutex decumbens, ramis prostratis radicantibus. Rami p. 461 annui virides glabri. Vernatio equitans. Folia *novella* glabra bicoloria, sciz. viridia basi ferruginea. Stipulae parvae ovatae obtusae integrae convexae strictae: margine interiore glandulis albis obsito, omnino ut in *S. lucida*. Folia *matura* ovata acuta glabra serrata; serraturis glandula spherica lutea terminatis, supra viridia, subtus pallidiora.

Place.—Found in July 1762 on the east side of the high mountain of White-Coom-Edge, in the head of Annandale. It grows there, more than 400 feet above the place where the *S. lapponum* grows on the same mountain. It is therefore a true alpine Willow, and yet I found it since in wet-moorish grounds, upon the estate of Cluny in Fife, not six hundred feet above the sea.

p. 462. XIX. *Salix lucida*.

S. foliis crenatis glaberrimis ovatis acutis, crenis glandulosis, stipulis ovatis intus glandulosis.

Salix Alpina pumila, repens, retuso Serpyllifolio lucido. Boccon. Mus., pars 2, p. 19, tab. 1?

Descriptio.

Frutex humilis, ramis prostratis radicantibus. Rami annui rubro-virides glabri. Vernatio equitans. Folia *novella* unicoloria viridia glaberrima. Stipulae parvae ovatae obtusae integrae convexae strictae, superficie et margine interiori glandulis albis obsito. Omnino ut in *S. vacciniifolia*. Folia *matura* ovata acuta glaberrima crenata, crenis glandulosis, supra saturate viridia lucida, subtus pallidiora. Margo folii prope basin integer, sed ad ipsum apicem glandulosus. Amenta foeminea tenuia cylindrica, at sine mare infertilia.

Place.—This, with other live Willows, was brought from the King's garden at Copenhagen, by the late Mr James Wright, surgeon, who, much to the loss of his friends and of natural history, fell by a premature death in the East Indies.

p. 464. XX. *Salix Evoniae*.

S. foliis glabris obovatis, serraturis glandulosis subtus glaucis exstipulaceis.

Salix pumila, foliis ovalibus, obscure serratis, utrinque laevibus, inferne glaucis. Gmelin, *Flor. Sib. tom.*, 1, p. 159, t. 35, p?

The Evon Willow.

Descriptio.

Frutex pedalis bipedalis, decumbens, ramosissimus, ramis brevibus.

Rami annui teretes subrubri, annotini lutescentes folia obovata, obtusa serrata, serraturis glandulosis supra viridia, glabra, subtus glauca, non autem villosa. Latera folii aequalia. Nerva media rubescens, glandulae duae minutissimae, loco stipularum folia interdum acuta praesertim ramis floriferis.

Mas.—Amentum semiunciale subterminale. Involucrum triphyllum, foliolis inaequalibus, lanceolatis, margine piloso serrulato. Nectarium bifidum. Stamina duo, antherae luteae.

Foemina.—Amentum sesquiunciale subterminale. Involucrum triphyllum, foliolis inaequalibus, lanceolatis. Squamae calycinae, nigrae cillosoe, nectarium glandula cylindracea minima, truncata, in axilla capsulae—capsulae laxae villosae.

p. 465. *Place*.—It grows in many places upon the riven Evon, in the head of Annandale, and particularly below Evon bridge, on the road from Moffat to Dumfries. Also near Strathevon in Clydesdale.

p. 467. XXII. *Salix linearis*.

S. foliis subserratis linearibus acutis distichis planis, subtus tenuissime villosis.

Salix minime fragilis, foliis longissimis utrinque viridibus. *Raj. syn.*, p. 449, n. 14.

p. 468. *Salix Rubra*, foliis integerrimis glabris lineari-lanceolatis acutis. *Huds. Flor. Angl.*, p. 428, n. 12.

Angl. Stone Rod. Horn Rod.

Descriptio.

Rami annotini rubri glabri.

Arbor mediocris. Stipulae duae lineari-ovatae.

Vernatio revoluta.

Foemina.—Amenta subterminalia ovata sursum secunda. Involucrum foliolis 5 lanceolatis integris villosis. Squamae

nigrae albo-villosae. Stigmata luteo-viridia. Floret 20 Martii dum vernat.

Place—It grows naturally in the wood of Caerlaverock in Nithsdale, and is planted in the hedges in the neighbourhood. It grows also about Craigiehall in West Lothian but in a cultivated state.

1. From the examination of this plant in Buddle's *Hortus siccus*, in the British Museum, there can be no doubt of its being the above species of Ray and Hudson, though the leaf is evidently serrated.

The following are new names, mostly illegitimate or *nomina nuda*, found in Walker's published works.

ESSAYS ON NATURAL HISTORY AND RURAL ECONOMY.

70 *Ulmus atinia*; 76 *Salix amerina*; 186 *Phasganon Columbae*; 188 *Bombycina Pinea*; 190, *Bombycina foeniculacea*, comb. nov. based on *Conferva foeniculacea* Huds.

ECONOMICAL HISTORY OF THE HEBRIDES AND HIGHLANDS OF SCOTLAND.

Vol. 1, 225 *Hordeum hybernum*; 227 *Triticum trimestre*; 232 *Triticum conicum*, *Triticum ramosum*; 244 *Cucubalus maritimus*; 342 *Carduus viarum*; 346 *Carex gigantea*, *Carex trigona*; 365 *Carex attenuata*, *Carex ballonensis*, *Carex polygamia*; 366 *Carex turgida*; 372 *Carex maritima*, *Carex oscaris*, *Festuca gallovidiensis*, *Plantago carnosa*, *Poa flabellifera*, *Raphanus maritimus*; 380 *Salix hebridiana*; 385 *Juncus flexuosus*.

Vol. 2, 23 *Avena nodosa*; 33 *Carex elata*, *Carex nemorosa*; 265 *Salix polygamia*; 274 *Salix amnicola*, *Salix Helix*; 278 *Juncus umbratilis*.

In the bibliography appended to this paper, several excellent biographical sketches of this remarkable Scot are included. That he was a notable man of his time, with a wide circle of influential and distinguished friends, is obvious from these accounts. He travelled widely on various commissions to remote parts of Scotland, particularly to the Western Isles. His essays, though chiefly concerned with the natural products, antiquities and inhabitants, with remarks on their ethnology, habits and diseases, have wide scientific interest. In addition to his botanical pursuits, he made

original observations on minerals,* fossils, birds and mammals and described new species of insects, molluscs and a sponge from Iona. He was in correspondence with many eminent naturalists of his time including Linnaeus with whom he shared a common interest in classification. That he did not always agree with Linnaeus is evident from a letter to Lord Kames written from Moffat on 18th February, 1773. This contains a censure of Linnaeus's arrangement of animals in the following terms: "Yet, to raise Monkeys to Men; to degrade Men to Monkeys; to attempt to annihilate or even to extenuate the line of partition between

*Headrick in his *View of the mineralogy, agriculture, manufactures and fisheries of the Island of Arran, with notices of antiquities* (1807), pp. viii and ix, states that he "has annexed descriptions of the rocks which occurred, by the late Dr. Walker, who may be justly reckoned the father of Mineralogy in this country. These were dictated in Latin, a few months before his death; and are a summary of more than twenty volumes of remarks on minerals, collected by the Doctor during his long and laborious life. It was edifying to behold a man, venerable by years and useful labours, after he was stone-blind, was worn down by indisposition and by domestic affliction, stifling his inward sorrows, and displaying all the ardour of youth in scientific pursuits."

Headrick also refers to Walker in his *General View of the Agriculture of the County of Angus, or Fifeshire* (1813). On p. 14 it is said that Walker had Porcelain Stone from the Pentland Hills "ground down at the potteries, and fabricated into Porcelain ware, of great beauty". According to Headrick (p. 327), Walker "was in the habit; especially during years of scarcity, of using yams in place of bread, in his own family. He cut them into thin slices, and either branded them on the fire, or dressed them in the frying pan, with as much butter as prevented the pan from burning. When dressed in this way, their taste was very pleasant; and they were used in all cases where bread is commonly used." The name "yam" or "Surinam" potato was used at this time for a coarse cattle potato. There is an interesting observation (p. 366) that Walker "generally covered his fruit trees, in spring, with old herring nets, or any other kinds of nets he could procure. He was decidedly of opinion . . . that these nets kept off the frost from the tender flowers and prevented their destruction".

Earlier recognition of Walker's contribution to the study of minerals was made in 1798 by Jameson who was his successor as Professor of Natural History. Jameson inscribed his work *An Outline of the Mineralogy of the Shetland Islands and of the Island of Arran* to Walker "in testimony of the great respect and sincere affection of his humble servant". Walker is frequently quoted in the text.

them, is a reigning taste in philosophy, which gives me great disgust. Linnaeus has long ranked us in the same order of animals with the Bat; and though in this article I perhaps justify his method, as much as any individual of my species, yet I could never look at it without umbrage. He still placed Man however in a genus by himself at the head of the system. He stickled a little indeed for combining us with the Orang-Outang; but finding that the creature had a *membrana nictitans*, he allowed him to remain with his companions. This was well enough. But his behaviour in his last book is truly provoking. He has there given us a brother-german—a *Homo Lar* forsooth!—some little scoundrel of a monkey, picked up in the woods of Macassar, whose very name I have in such detestation, that I am persuaded I am not a drop's blood to him.

“Let your Lordship pursue the analogy between Plants and Mankind, so far as you will, it is not likely I shall be as much offended, as with my friend Linnaeus. I have been from the cradle fond of vegetable life; and though I like my species, and the rank I hold in the creation, I declare I would sooner claim kindred to an oak or apple-tree than to an ape.”

I have not mentioned all the references to Walker which I have traced but I cannot pretend that my search has been complete nor even have I been able to give proper study to the manuscripts and letters available. There may well be serious omissions and oversights in my appraisalment but my main purpose will be served if belated credit is ensured to one eminent Scot on the occasion of doing honour to another.

I am indebted to the Council of the Linnean Society for permission to reproduce in facsimile (Plate I) a sheet from one of Walker's letters to Pulteney. The portrait of Walker (Plate II) is from an engraving illustrating the memoir by Sir William Jardine in the *Naturalist's Library*.

My colleagues Mr. Hubbard and Miss Skan have very kindly and laboriously checked my references to new species and names and I am grateful to Mr. Atkinson for his skilful photographic reproductions of Walker's handwriting and portrait.

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